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AN INTRODUCTION

TO

NEUROLOGY

BY

C. JUDSON HERRICK

PROFESSOR OF NEUROLOGY IN THE UNIVERSITY OF CHICAGO

THIRD EDITION, THOROUGHLY REVISED

PHILADELPHIA AND LONDON

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PREFACE TO THE THIRD EDITION

THERE are two groups of functions performed by the nervous system which are of general interest; these are, first, the physiological adjustment of the body as a whole to its environment and the correlation of the activities of its organs among themselves, and, in the second place, the so-called higher functions of the cerebral cortex related to the conscious life. The second of these groups of functions cannot be studied apart from the first, for the entire conscious experience depends for its materials upon the content of sense, that is, upon the sensory data received by the lower brain centers and transmitted through them to the cerebral cortex. Since the organization of these lower centers is extremely complex, and since even the simplest nervous processes involve the interaction and coöperation of several of these mechanisms, it follows that an understanding of the workings of any part of the nervous system requires the mastery of a large amount of rather intricate anatomical detail.

Fortunately, the knowledge of the precautions which must be observed in order to maintain the nervous system in healthy working order is not difficult of acquisition (though surprisingly few people seem to have gained it), just as any one can learn to operate an automobile, even though quite ignorant of the engineering problems involved in its design and construction. Information regarding these matters of practical hygiene is readily available,[1] and it is not the primary purpose of this book to supply it. But to understand the actual inner operation of the nervous mechanisms is a much more difficult matter, and this knowledge cannot be acquired without arduous and sustained study of the peculiar form relations of the nervous organs and their complex interconnections; and information of this sort is indispensable for a grasp of the prin-

[1] See the Bibliography on page 13.

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ciples of nervous organization, and especially for an intelligent treatment of nervous diseases.

The study of neurology is, therefore, intrinsically difficult if one is to advance beyond its most superficial phases; the more so if the student is not well grounded in general biology and at least the elements of the general anatomical structure of the vertebrate body. To these inherent difficulties there is added a purely artificial obstacle in the form of a cumbersome and confused terminology which has grown up during several centuries of anatomical study of the brain, in the early stages of which little or no comprehension of the functional significance of the parts discovered was possible, and fanciful or bizarre names were given without reference to the mutual relationship of parts.

The problems which at present chiefly occupy the attention of neurologists are of three sorts—first, to discover the regional localization within the nervous system of the nerve-cells and fibers which serve particular types of function or, briefly, architecture; second, to discover the chemical or other changes which take place during the process of nervous function, that is, the metabolism of the nervous tissues, and third, how to keep the nervous system in health and to diagnose and cure diseased conditions. The first of these problems is at present further advanced than the second; the larger part of this work is, therefore, devoted to a description of architectural relations. Without a knowledge of these relations, moreover, the problems of function cannot be approached. The medical problems of the third group depend upon both of the others; with these, however, this book is not concerned.

It is impossible to understand clearly the form of the brain, and especially the relations of its internal structures, from verbal descriptions merely. Pictorial illustrations and the various brain models which are on the market are of great assistance; but actual laboratory experience in dissecting the brain and, if possible, the study of microscopic preparations of selected parts of it are indispensable for a thorough mastery of the subject. The brains of the sheep, dog, and cat are easily obtained, and are so similar to the human brain in all respects, save the smaller relative size of the cerebral cortex,

that they can readily be used for such studies. Before dissection the brain should be carefully removed from the skull and hardened by immersion for a few days in a solution of formalin (to be obtained at any drug store and diluted with water in the proportion of one part formalin to nine parts water). Several neurological laboratory guides have been published, and one of these should be followed in the dissection.[1]

The structure and functions of the nervous system are of interest to students in several different fields—medicine, psychology, sociology, education, general zoölogy, comparative anatomy, and physiology, among others. The view-points and special requirements of these various groups are, of course, different; nevertheless the fundamental principles of nervous structure and function are the same, no matter in what field the principles are applied, and the aim here has been to present these principles rather than any detailed application of them.

The materials presented in this book are arranged in three groups: (1) Chapters I to VII discuss the more general neurological topics; (2) Chapters VIII to XVIII comprise a brief account of the form of the nervous system and the functional significance of its chief subdivisions in general, followed by a review of the architectural relations of the more important functional systems; (3) Chapters XIX to XXI are devoted to the cerebral cortex and its functions. Readers whose chief interest lies in the general neurological questions may omit much of the detail comprised within the second group of chapters or use these for reference only. To facilitate ready reference the general index has been prepared with especial care, and with it is combined a brief glossary of some more commonly used technical terms. In the text some of the more special topics, which may be omitted if a briefer presentation is desired, are printed in smaller type.

The third edition, like the second, does not depart from the original plan of the work, an introduction in the literal sense. References to important recent works are added, but the temptation greatly to increase the size of the book has been steadfastly resisted. Several excellent text-books and atlases

[1] See the Bibliography on page 13.

are available (some very recently published), and to these the reader is referred for the illustrations and more detailed descriptions necessary to complete the rather schematic outline here presented. To the medical student it is doubtless a great convenience to assemble within the covers of one book all of the essential facts relating to the nervous system which he is expected to master in his required courses; but in the author's experience this is not an unmixed benefit. A smaller work which helps the student to organize his knowledge in definite functional patterns early in his course and which at the same time demands constant reference to numerous larger books of reference may give a better preparation and a wider outlook.

C. JUDSON HERRICK.

CHICAGO, *July*, 1922.

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INTRODUCTION TO NEUROLOGY

CHAPTER I

BIOLOGICAL INTRODUCTION

THE living body is a little world set in the midst of a larger world. It leads in no sense an independent life, but its continued welfare is conditioned upon a nicely balanced adjustment between its own inner activities and those of surrounding nature, some of which are beneficial and some harmful. The great problem of neurology is the determination of the exact part which the nervous system plays in this adjustment.

This problem is by no means simple. The search for its solution will lead us, in the first place, back to an examination of some of the fundamental properties of the simplest living substance, of protoplasm itself; and in the last analysis it will involve a consideration of the highest mental capacities of the human race and of the physiological apparatus through which these capacities come to expression. We shall first take up the nature of this adjustment on the lower biological levels.

All of the infinitely diverse forms of living things have certain points in common, so that one rarely has any doubt whether a given object is alive or dead. Nevertheless, the precise definition of life itself proves very difficult. Herbert Spencer, in his "Principles of Biology," after many pages of close argument and rather formidable verbal gymnastics, arrived at this formula: Life is "the definite combination of heterogeneous changes, both simultaneous and successive, in correspondence with external coexistences and sequences;" or, more briefly, "The continuous adjustment of internal relations to external relations." A somewhat similar idea was subsequently more simply expressed by the late C. L. Herrick

in the proposition, "Life is the correlation of physical forces for the conservation of the individual"; and this, in turn, may be cast in the more general form, Life is a system of forces maintained by a continuous interchange of energy between the system and its environment, these forces being so correlated as to conserve the identity of the system as an individual and to propagate it. A certain measure of modifiability in the character of the system, without loss of its individuality, is not excluded. Child has recently formulated a definition of life in dynamic terms as follows, "A living organism is a specific complex of dynamic changes occurring in a specific colloid substratum which is itself a product of such changes and which influences their course and character and is altered by them" (Senescence and Rejuvenescence, Chicago, 1915, p. 26).

No one of these definitions, or any other which has been suggested, is fully satisfactory; but biologists generally agree that the common characteristics of living beings can best be expressed in the present state of our knowledge in terms of their actions, their behavior. The properties commonly ascribed to any object are in last analysis names for its behavior, and the so-called vital properties are very special forms of energy transformation.

Now, the chief difference between a corpse and a living body consists in the fact that the forces of surrounding nature tend to the disintegration of the dead body, while in the living body these forces are utilized for its upbuilding. If, then, the vital process is essentially a special type of mutual interaction between the bodily mechanism and the forces of the surrounding world, of the correspondence between the organism and the environment, to use the Spencerian phrase, it follows that the living body cannot be studied by itself alone. Quite the contrary, the analysis of the environmental forces upon which the life of the body depends and of the parts of the body itself in their relations to these external forces is the very kernel of the problem of life.

The measure of the fulness of life in any organism is twofold. In the first place, the life is measured by the amount of energy which the organism can assimilate from surrounding

nature and incorporate into its own organization. This enters the body chiefly in the form of chemical potential energy in food eaten, air breathed, and so on, and can be quantitatively determined and stated in the form of standard units of energy, such as calories or foot-pounds of work. This measures the working capacity of the machine, but gives little insight into the real value of the work done. In the second place, life may be measured in terms of the extensity or number and diversity of environmental relations. This takes account of the range or working distance of the organization and, in general, of the efficiency of the work done. For evidently the organism which has few and simple relations with the environment, so that it can adjust itself to only a small range of external conditions, is less efficient than one which has many diverse relationships and an extensive series of possible adjustments, even though the actual amount of energy expended may be vastly greater in the former than in the latter case. The first of these standards is a tolerably satisfactory measure of the vegetative functions of the body, sometimes less happily termed the "organic functions." We have no word in common use which covers precisely the group of activities embraced by our second standard of measurement, though the terms "animal functions," "somatic or exteroceptive activities" are sometimes used in about this sense.

Let us now endeavor to illustrate the last topic a little more concretely. We are standing on a hilltop overlooking a meadow, through which runs a mountain brook, and beyond the valley is another range of rugged hills. In the fence-corner near us is a patch of daisies and clover with a honey-bee buzzing from flower to flower. A plowboy is crossing the field, and at our elbow an artistic friend is busy with sketching pad and brushes. The owner of the farm waves a greeting as he drives past. Here are five things which have this at least in common, that they are alive—daisy, bee, plowboy, artist, and the proprietor of the estate. There can be no doubt about their vitality, but how differently they respond to the sunshine, the rain, and the other forces of nature.

The daisy expands in the vivifying light of the summer sun, the energy of whose actinic rays is used to build up living

protoplasm and vegetable fiber from the inert substances of air and soil. Its vitality, measured in terms of energy transformation, is great; yet how limited its range of life, how helpless in the face of the storms of adversity which are sure to buffet it. Rooted to its station, it can only assimilate what food is brought to it and it cannot flee from scorching wind or blighting frost.

The honey-bee leads a more free and varied life. Instead of passively and blindly waiting for such bane or blessing as fate may bring, she hurries forth, strong of wing and with senses alert, to gather the daily measure of honey and pollen. The senses of touch, sight, and smell open realms of nature forever closed to the plant, and enable her to seek food in new fields when the local supply is exhausted, as well as to avoid enemies and misfortunes. With the approach of the storm, she flies to shelter in a home which she and her sisters have prepared with consummate skill. Yet in this provision for the future in hive and well-stocked honeycomb there is little evidence of intelligent foresight or rational understanding of the purposes for which they work. Though so much more highly organized than the plant, the honey-bee is to a very large extent blindly following out the inborn impulses of her hereditary organization and she has no clear understanding of what she does, much less why she does it. There is some evidence of intelligent adaptation in her behavior, but the part played by this factor in her life as a whole is probably very small compared with the blind inborn impulses which dominate most of her activities. Like the plant, the bee's reactions are determined chiefly by the past evolutionary history of the species, which has shaped the innate organization of the body and fixed its typical modes of response to stimulation. But the bee lives much more in the present than does the plant; that is, she can vary her behavior much more widely in response to the needs of the moment. As for the future, she knows naught of it.

The farmer's boy whistles as he goes about his work. He, too, has a certain innate endowment, including the whole range of his vegetative functions, together with an instinctive love of sport and many other inborn aptitudes. This is his inheritance from the past. By these instincts and appetites

he is, as Dewey says, "pushed from behind" through the performance of many blindly impulsive acts. He is a creature of the present, too, his whole nature overflowing with the joy of living. But he also looks into the future and hastens through the daily tasks that he may obtain the coveted hour of sunset to fish in the brook. He flicks off the heads of the daisies with his whip-stock and remarks in passing, "This meadow is choking up with white-weed. The boss will have to plow it up next year and replant it." The extraordinary natural beauty of the place is, however, unnoticed amid the round of daily work and simple pleasure.

The artist looks out upon the same scene, but through what different eyes! The mass of white daisies and the rocky knoll beyond ruddy with sheep sorrel suggest to him no waste of valuable pasture land, but a harmony of color and grace of form upon which he feasts his soul. The esthetic delights of the forest, the sky, the brook, and the overhanging crag beyond are for him unmixed with any utilitarian motive.

Finally, the owner turns a critical eye upon his meadow, appraising it as part of an entire estate. For him it has value as a commercial asset measured in terms of tons of hay per acre, as an esthetic asset measured in terms of appreciation of scenic beauty, as part of a family inheritance to be conserved for his heirs, and as a responsibility to be developed and improved as a social obligation. He manifests a pride of ownership and the whole face of nature in his valley is changed to conform to his ideal.

Each of these five organisms occupies, in one sense, the same environment; but it is evident that the factors of this environment with which each comes into active vital relations are immeasurably different. They correspond with or are attuned to quite different energy complexes, though the correspondence or interaction is very real in each case. This has been stated very simply by Dr. Jennings when he says that every species of organism has its characteristic "action system," *i. e.*, a habitual mode of reaction to its environment which is determined wholly or in part by its inherited organization.

Every animal and every plant has, accordingly, a definite

series of characteristic movements which it can make in response to external stimulation. This is all that Jennings means by the "action system." We humans are no exception to this rule of life. We move along in a more or less stereotyped way, through more or less familiar grooves, in our daily work. Much of this work is routine, done about as mechanically as the flower unfolds its petals to the morning sun or the honey-bee gathers in her store of honey. This is our action system. Of course, we have much else to do besides this routine, and our actual value to the community is in large measure determined by our ability to vary this routine in adaptation to new situations as they arise. Even the daisy has a little of this capacity for independently variable action; the insect has more; and man's preëminence in the world is due primarily to his larger powers of adapting his reactions not only to the needs of the moment, but to probable future contingencies, *i. e.*, of varying his inborn action system by intelligently directed choices.

This distinction between the blind working of a stereotyped action system whose character is determined by the inherited bodily structure, on the one hand, and individually acquired variable adaptive actions (which may or may not be intelligently performed), on the other hand, is very fundamental, and we shall have occasion to return to it. Most animal activities contain both of these factors, and it is often very difficult to analyze a given example of behavior into its elements, but the distinction is nevertheless important. Plant life is characterized by the dominance of invariable types of reaction which are determined by innate structure; these in their most elementary forms give us, in fact, the so-called vegetative functions. These same functions predominate in the lowest animals also; but in the higher animals, as we shall see, there are two rather distinct lines of evolutionary advance. In one line the innate stereotyped functions are very highly specialized, leading up to a complex instinctive mode of life; in the other line these functions are subordinated to a higher development of the individually acquired variable functions, leading up to the intelligence and docility of the higher mammals, including the human race.

The distinction between plants and animals is very difficult to draw and, in fact, there are numerous groups of organisms which at the present time occupy an ambiguous position, such as the slime molds. The botanists claim them and call them Myxomycetes; the zoölogists also describe them under the name Mycetozoa; still other naturalists frankly give up the problem and assign them to an intermediate kingdom, neither vegetable nor animal, which they call the Protista. As children we probably considered the chief distinction between plants and animals to be the ability of the latter to move freely about; but one of the first lessons in our elementary biology was the correction of this notion by the study of sedentary animals and motile plants. Nevertheless, I fancy that in the broad view the childish idea has the root of the matter in it. The plants and sedentary animals may have their vegetative functions of internal adjustment never so highly specialized and yet remain relatively low in the biological scale because their relations with the environment are necessarily limited to the small circle within which they first take root, whereas the power of locomotion carries with it, at least potentially, the ability to choose between many more environmental factors. It is only the free-moving animals that have anything to gain by looking ahead in the world, and here only do we find well-developed distance receptors, *i. e.*, sense organs adapted to respond to impressions from objects remote from the body. And the distance receptors, as we shall see, have dominated the evolution of the nervous system in vertebrates and determined the lines it should follow.

The net result of this discussion can be briefly stated. The differences between various kinds of organisms are, in the main, incidental to the extent and character of their relations with the forces of surrounding nature. A species which can adjust itself to few elements of its environment we call low; one that can adapt itself to a wide range of environmental conditions in a great variety of ways we call higher. The supremacy of the human race is directly due to our capacity for diversified living. If man finds himself in an unfavorable climate, he may either move to a more congenial locality or adapt his mode of life by artificial aids, such as clothing, houses, and fire. And in these

adaptations he is not limited to a narrow range of inherited instincts, like the hive of bees, but his greater powers of observation and reflection enable him to discover the general uniformities of natural process (he calls these laws of nature) and thus to forecast future events and prepare himself for them intelligently. In other words, to return to our original point of view, our advantage in the struggle for existence lies in our ability to correlate our bodily activities with a wide range of natural forces so as to make use of these forces for our good rather than our hurt. (Of course, it should be borne in mind that this formula makes no pretense of being an exhaustive account of human faculty; but only that, in so far as biological evolutionary factors have operated in the human realm, they act in accordance with this principle.) The apparatus by which these external adjustments are effected and by which the inner parts of the body are kept in working order is the nervous system.

CHAPTER II

THE NERVOUS FUNCTIONS

THE body is composed of organs and tissues, the organs being parts with particular functions to perform and the tissues being the cellular fabric of which the organs are composed. The tissues (which must be studied microscopically) are classified, sometimes in accordance with the general functions which they serve, such as the nervous and muscular tissues, and sometimes with reference to the forms and arrangements of their component cells. An illustration of the latter method of treatment is furnished by the epithelial tissues, which are thin sheets of cells, sometimes arranged in one layer (simple epithelia), sometimes in several layers (stratified epithelia). Epithelial tissues may perform the most diverse functions.

All living substance (protoplasm) possesses in some measure the distinctive nervous functions of excitability and conductivity, that is, it responds in a characteristic fashion to certain external forces (stimuli), and when thus stimulated at one point the movement or other response may be effected by some remote part. This last feature implies that some form of energy is conducted from the site of the stimulus to the part moved. Ordinary protoplasm also possesses the power of integration, that is, of combining a number of individual reactions to stimulation in diverse special adjustments so as to promote the welfare of the body as a whole.

The physiological mechanisms of these fundamental protoplasmic properties are very complex and as yet only imperfectly understood. The experiments of Child have shown that one important factor common to all of them can be reduced to quantitative expressions of differences in the rate and amount of chemical change involved in the processes of excitation and conduction. He has explained (1915) how physiological gradients in this type of metabolism by correlated interaction form the dynamic basis of the integrating or unifying forces which maintain the individuality of the organism, and in a recent work (1921) he has made a detailed study of the applications of this principle in the nervous system, thus outlining the history of the differentiation of the nervous tissues

from more generalized kinds of protoplasm. Parker (1919) has investigated the latter problem from a different point of view.

The one-celled animals and all plants lack the nervous system entirely; nevertheless they are able to make highly complex adjustments. The leaves, roots, and stems of the higher plants have individual functions which are, however, bound together or integrated into a very perfect unity. In animals, as contrasted with plants, we see a further differentiation of parts of the body for special functions, and at the same time a more perfect correlation of part with part and integra-

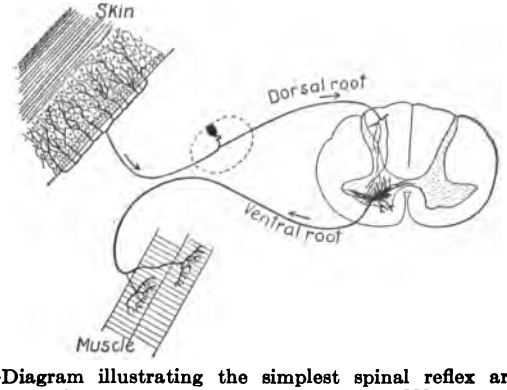

Fig. 1.—Diagram illustrating the simplest spinal reflex arc consisting of two nervous elements or neurons (see Chapter III), a sensory neuron connected with the skin and a motor neuron connected with a muscle. Physiological connection between the two neurons is effected within the spinal cord. (Modified from Van Gehuchten.)

tion of the whole for rapid and diversified reactions of the entire body. The nervous system is the apparatus of these more perfect adjustments and its protoplasm is highly modified in different directions. Some parts may be especially sensitive to particular forms of energy (such as light waves, sound waves, etc., this being termed the adequate stimulus in each case); other parts, the nerves, are highly modified so as to conduct nervous impulses from part to part with a minimum expenditure of energy and loss of efficiency; still other parts of the nervous system serve as centers for receiving and redistributing nervous impulses somewhat after the fashion of the

central exchange of an automatic telephone system. These are the correlation centers, and they are larger and more complex in proportion to the range of diversity in the possible reactions of the animal.

The simpler reactions to stimulation of the sort here under consideration are called *reflexes* (Fig. 1; see also p. 59), and the essential mechanism is a reflex arc consisting of (1) a sensitive receiving organ (receptor or sense organ); (2) a conductor (afferent or sensory nerve) transmitting the nervous impulse inward from the receptor; (3) a correlation center or adjustor, generally located within the central nervous system; (4) a second conductor (efferent or motor nerve) transmitting the nervous impulse outward from the center to (5) the effector apparatus, consisting of the organs of response (muscles, glands) and the terminals of the efferent nerves upon them.

No part of the nervous system has any significance apart from the peripheral receptor and effector apparatus with which it is functionally related. This is true not only of the nervous mechanism of all physiological functions, but even of the centers concerned with the highest manifestations of thought and feeling of which we are capable, for the most abstract mental processes use as their necessary instruments the data of sensory experience directly or indirectly, and in many, if not all, cases are intimately bound up with some form of peripheral expression.

The neurologist's problem is to disentangle the inconceivably complex interrelations of the nerve-fibers which serve all the manifold functions of adjustment of internal and external relations; to trace each functional system of fibers from its appropriate receptive apparatus (sense organ) to the centers of correlation; to analyze the innumerable nervous pathways by which these centers are connected with each other (correlation tracts); and, finally, to trace the courses taken by all outgoing impulses from these correlation centers to the peripheral organs of response (muscles, glands, etc., or, collectively, the effectors).

This is no simple task. If it were possible to find an educated man who knew nothing of electricity and had never heard of a telegraph or telephone, and if to this man was assigned the duty of making an investigation of the telegraph and

telephone systems of a great city without any outside assistance whatever, and of preparing a report upon all the physical equipment with detailed maps of all stations and circuits and with an explanation of the method of operation of every part, his task would be simple compared with the problem of the neurologists. The human cerebral cortex alone contains some 9280 million nerve-cells, most of which are provided with long nerve-fibers which stretch away for great distances and branch in different directions, thus connecting each cell with many different nerve-centers. The total number of possible nervous pathways is, therefore, inconceivably great.

Fortunately for the neurologists, these interconnecting nervous pathways do not run at random; but just as the wires entering a telephone exchange are gathered together in great cables and distributed to the switchboards in accordance with a carefully elaborated system, so in the body nerve-fibers of like function tend to run together in separate nerves or within the brain in separate bundles called *tracts*. Notwithstanding the complexity of organization of the nervous organs, the larger and more important functional systems of nervous pathways have been successfully analyzed, and the courses of nervous discharge from the various receptors to the appropriate centers of adjustment, and from these (after manifold correlations with other systems) to the organs of response, are fairly well known. The acquisition of this knowledge has required several centuries of painstaking anatomical and physiological study, and much remains yet to be done.

The external forms of the brain and other parts of the nervous system are dependent mainly upon the arrangements of the nerve-cells of which they are composed (for the characteristics of these cells see Chapter III), and these arrangements, in turn, are correlated with the functions to be performed. The functional connections of the nerve-cells can be investigated best by the microscopical study of the tissues combined with physiological experimentation. From this it follows that the study of the gross anatomy, the microscopical anatomy (histology), and the physiology of the nervous system should go hand in hand so far as this is practicable.

A study of the comparative anatomy of the nervous system shows that its form is always correlated with the behavior of

the animals possessing it. The simplest form of nervous system consists of a diffuse network of nerve-cells and connecting fibers distributed among the other tissues of the body. Such a nervous system is found in some jelly-fishes and in parts of the sympathetic nervous system of higher animals. Animals which possess this diffuse type of nervous system can perform only very simple acts, chiefly total movements of the whole body or general movements of large parts of it, with relatively

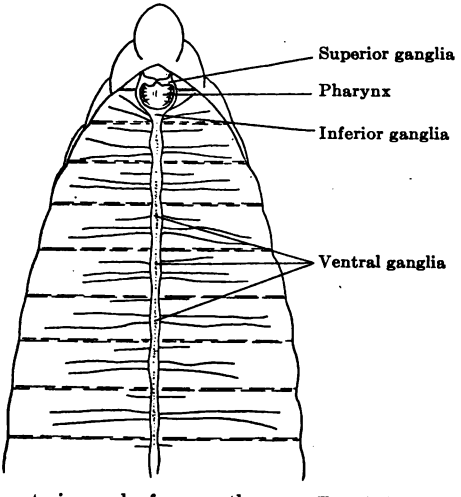

Fig. 2.—The anterior end of an earthworm (Lumbricus) laid open from above with all of the organs dissected away except the ventral body wall and ventral ganglionic chain.

small capacity for refined activities requiring the coöperation of many different organs. But even the lowest animals which possess nerves show a tendency for the nervous net to be condensed in some regions for the general control of the activities of the different parts of the body. Thus arose the central nervous system. (Some works dealing with the evolution of the nervous system are cited at the end of this chapter.)

The aggregations of nervous tissue to which reference has just been made, containing the bodies of the nerve-cells, are called *ganglia*,[1] and in all invertebrate animals the central

[1] On the ganglia of the vertebrate vervous system, see page 116.

nervous system is a series of such ganglia, variously arranged in the body and connected by strands containing nerve-fibers only, that is, by nerves.

The central nervous systems of all but the lowest forms of animals are developed in accordance with two chief structural patterns, represented in typical form by the worms and insects on the one hand, and by the back-boned animals or vertebrates on the other hand.

In the segmented worms (such as the common earthworm, Fig. 2) the central nervous system consists of a chain of ganglia connected by a longitudinal cord along the lower or ventral wall of the body. Each of these ganglia is connected by means of peripheral nerves with the skin and muscles of its own segment, and each joint of the body with its contained ganglion (ventral ganglion) has a certain measure of physiological independence so that it can act as a unit. This is a typical segmented nervous system. At the head end of the body the ventral ganglionic chain divides around the pharynx and mouth, and there are enlarged ganglia above and below the pharynx. The superior ganglia (supra-esophageal ganglia) are sometimes called the brain, and this organ dominates the local activities of the several segments, enabling the animal to react as a whole to external influences.

The nervous systems of crustaceans (crabs and their allies), spiders, and insects have been derived from the type just described. In these animals the segments of the body are more or less united in three groups, constituting respectively the head, thorax, and abdomen, and the ganglia of the central nervous system are modified in a characteristic way in each of these regions. Figure 3 illustrates the nervous systems of four species of flies, showing different degrees of concentration of the ganglia. In all cases the head part (brain) is greatly enlarged, and is arranged, as in worms, in ganglia above and below the mouth and esophagus. The other ganglia are diversely arranged, from the simple condition (*A*) where there are three thoracic ganglia, one for each pair of legs, and six abdominal ganglia, through intermediate stages (*B* and *C*), to the highest form (*D*), where all of the ganglia of both thorax and abdomen are united in a single thoracic mass.

The type of nervous system just described is found through-

out the highest groups of invertebrate animals, as in insects and spiders, and is constructed on a totally different plan from that of all of the vertebrate or back-boned animals. In this latter group we have, instead of a segmented chain of ventrally placed solid ganglia, a hollow tube of nervous tissue which extends along the back or dorsal wall of the body and constitutes the spinal cord and brain. The cavity or lumen of this tube extends throughout the entire length of the central nervous system, forming the ventricles of the brain and the central canal of the spinal cord. The details of the invertebrate nervous systems (whose structures are very diverse) will not be further considered in this work; the nervous systems of all vertebrates, however, are constructed on a common plan, and,

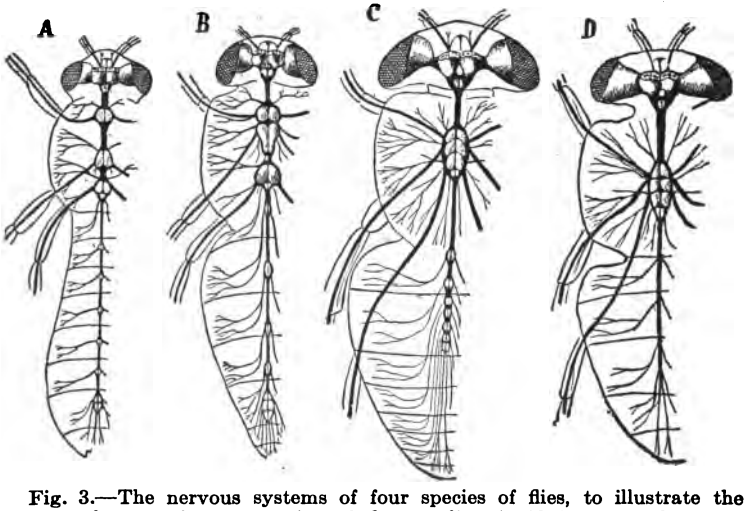

Fig. 3.—The nervous systems of four species of flies, to illustrate the various degrees of concentration of the ganglia: *A*, Chrionomus plumosus, with three thoracic and six abdominal ganglia; *B*, Empis stercorea, with two thoracic and five abdominal ganglia; *C*, Tabanus bovinus, with one thoracic ganglion and the abdominal ganglia moved toward each other; *D*, Sarcophaga carnaria, with all thoracic and abdominal ganglia united into a single mass. (After Brand, from Lang's Text-book of Comparative Anatomy.)

though our prime interest is the analysis of the human nervous system, we shall find that many of the details sought can be seen much more clearly in the lower vertebrates than in man.

Correlated with these differences between the structure of invertebrate and vertebrate nervous systems there are equally fundamental differences in the behavior of these animals which require a few words of further explanation. Living substance exhibits as its most fundamental characteristic, as we saw at the beginning, the capacity of adjusting its own activities to constantly changing environmental conditions in such a way as to promote its own welfare. This adjustment may be effected in two ways, both of which are universally present and which throughout the remainder of this work we shall call the *invariable* or innate behavior and the *variable* or individually modifiable behavior.

Every animal reaction, then, contains these two factors, the invariable and the variable or individually modifiable. The first factor is a function of the relatively stable organization of the particular living substance involved. The pattern of this organization is inherited, and these characteristics of the behavior are, therefore, common, except for relatively slight deviations, to all members of the race or species; they are rigidly determined by innate bodily organization so arranged as to facilitate the appropriate reactions, in an invariable mechanical fashion, to every kind of stimulation to which the organism is capable of responding at all. In the strictly vegetative functions, in all true reflexes (as these are defined on page 59), and in purely instinctive activities in general this factor of behavior is dominant.

But in addition to this invariable innate behavior, all organisms have some power to modify their characteristic action systems in adaptation to changed environmental relations. This individual modifiability is known as biological regulation, a process which has of late been very carefully studied. We cannot here enter into the problems connected with form regulation, that is, the power of an organism to restore its normal form after mutilation or other injury. On regulation in behavior reference should be made to the works of Jennings and Child. In lower organisms Jennings recognizes three factors in the regulation of behavior: First, the occurrence of definite internal processes; these form part of the invariable hereditary action system referred to above. Second, interference with these processes causes a change of behavior and

varied movements, subjecting the organism to many different conditions. Third, one of these conditions may relieve the interference with the internal processes, so that the changes in behavior cease and the relieving condition is thus retained. Lack of oxygen, for instance, would interfere with an animal's internal processes; this leads it to move about; if finally it enters a region plentifully supplied with oxygen, the internal processes return to normal, the movement ceases, and the animal again settles down to rest. If this regulatory process is oft repeated another factor enters, viz., the facilitation of a given adjustment by repetition. Thus arise physiological habits or acquired automatisms.

The more highly complex forms of individual modifiability are termed associative memory and intelligence, and the latter of these is by definition consciously performed. Whether consciousness is present in the simpler forms of "associative memory" as these are demonstrated by students of animal behavior in lower animals cannot be positively determined. In the behavior of lower animals there are no criteria which enable us to tell whether a given act is consciously performed or not, and, therefore, the lower limits of intelligence in the animal kingdom are problematical. In other words, the manifestations of variable behavior form a graded series from the simple regulatory phenomena of unicellular organisms, as illustrated above, to the highest human intelligence, so far as these express themselves objectively.

In mankind, where intelligent behavior is dominant, the stereotyping of the adjustments by repetition (true habit formation) may also take place, and in this case the acquired automatisms are sometimes said to arise by "lapsed intelligence," that is, an act which has been consciously learned may ultimately come to be performed mechanically and nearly or quite unconsciously. Much of the process of elementary education is concerned with the establishment of such habitual reactions to frequently recurring situations. How far "lapsed intelligence" is represented in the so-called instincts of other animals is still a debated question (see p. 338).

Among the invertebrate animals, the insects and their allies possess a bodily organization which favors the performance of

relatively few movements in a very perfect fashion, that is, the action system is simple but highly perfected within its own range. Their reflexes and instincts are very perfectly performed, but the number of such reactions which the animal can make is rather sharply limited and fixed by the inherited bodily structure. Their behavior is dominated by the invariable and innate factors and they cannot readily adapt themselves to unusual conditions. The vertebrates likewise have many elements of their behavior which are similarly fixed

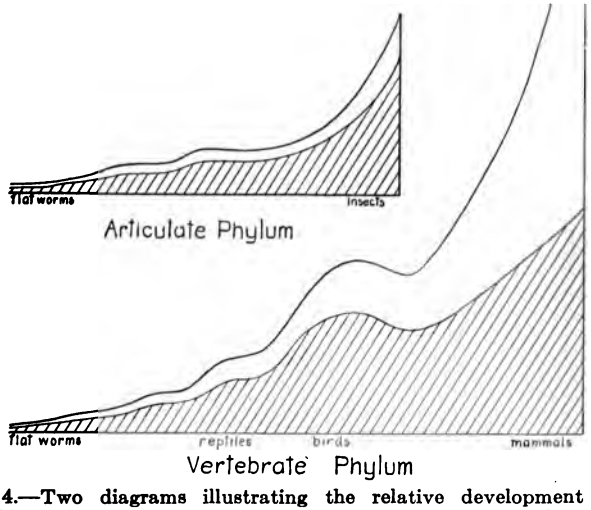

Fig. 4.—Two diagrams illustrating the relative development of the invariable and variable factors in the behavior of the articulate phylum and the vertebrate phylum of the animal kingdom. In the articulate phylum the invariable factor (represented by the shaded area) predominates throughout; in the vertebrate phylum the invariable factor predominates in the lower members of the series, and the variable factor (represented by the unshaded area) increases more rapidly in the higher members, attaining its maximum in man, where intelligence assumes the dominant rôle.

or stereotyped in their innate organization; but, in addition to these stable reflexes and instincts, the higher members of this group have also a considerable capacity for individual modifiability in behavior, and they are characterized by greater individual plasticity and docility (Yerkes). It appears that the tubular type of nervous system found in vertebrates permits of the development of certain kinds of correlation

mechanisms which are impossible in the more compact form of ganglia of the insects. These two branches of the animal kingdom have, therefore, during all of the more recent evolutionary epochs diverged farther from each other, and now, in their highly differentiated conditions, neither type could be derived from the other. The jointed animals (articulates) developed from the lower worms, and this branch of the animal kingdom, which may be called the articulate phylum, culminates in the insects. The vertebrates were probably developed from similar lowly worm-like forms along an independent line of evolution, and this branch of the animal kingdom, the vertebrate phylum, culminates in the human race. Figure 4 illustrates in a rough diagrammatic way the relative development of the variable and invariable factors of behavior in the articulate and vertebrate phyla.

In unicellular organisms without nervous systems the general protoplasm, of course, is the apparatus of both the invariable and the variable factors of behavior, and the simpler forms of nervous system likewise possess both of these capacities. But in the more complex forms of nervous system among vertebrates special correlation centers are set apart for the variable activities, particularly those which are intelligently performed, and the most important of these centers are found in the cerebral cortex. This is the part of the brain which is greatly enlarged in mankind, as contrasted with all other animals, and the last three chapters of this work are devoted to the structure and functions of these cortical mechanisms with whose activity the progress of human culture is so intimately related.

It should be borne in mind that the higher correlation centers which serve the individually variable or labile behavior in higher vertebrates can act only through the agency of the lower reflex centers. The point is, that all of the *elements* of behavior are represented in the innate neuro-muscular organization. Every single act which the animal is capable of performing has its mechanism provided in the inherited structure. But higher animals may learn by experience to combine these simple elements in new patterns. The higher correlation centers serve this function. The presence and general arrangement of these centers is, of course, also de-

termined in heredity; but the particular associations which will be effected within them are determined by individual experience, and the building up of these new associations is the chief business of education (see p. 349). In the analysis of behavior and the related neurological mechanisms the distinction between the innate and the individually acquired factors must always be kept clearly in mind. The failure to do so, and also the failure to distinguish between these two factors and the acquired automatisms (p. 33), is responsible for much confusion in the current discussions of instinct.

In the nomenclature of the correlation centers there is considerable diversity of usage. In describing the adjustments made by these centers neurologists frequently use the words coördination, correlation, and association in about the same sense; but the adjustments made in those centers which lie closer to the receptors or sense organs are physiologically of different type from those made in the centers related more closely to the effector apparatus. In recognition of this fact the following usage has been suggested to me by Dr. F. L. Landacre and will be adopted in this work:

The term *correlation* is applied to those combinations of the afferent impulses within the sensory centers which provide for the integration of these impulses into appropriate or adaptive responses; in other words, the correlation centers determine what the reaction to a given combination of stimuli will be. Nervous impulses from different receptors act upon the correlation centers, and the reaction which follows will be the resultant of the interaction of all of the afferent impulses (and physiological traces or vestiges of previous similar responses) involved in the process. When this resultant nervous discharge passes over into the motor centers and pathways, the final common paths (pp. 62, 65) innervated will lead to a response whose character is determined by the organization of the particular motor centers and paths activated.

To the term *coördination* we shall give a restricted significance, applying it only to those processes employing anatomically fixed arrangements of the motor apparatus which provide for the co-working of particular groups of muscles (or other effectors) for the performance of definite adaptively useful responses. Every reaction—even the simplest reflex—involves the combined action of several different muscles, and these muscles are so innervated as to facilitate their concerted action in this particular movement. These are called synergic muscles. Coördination involves those adjustments which are made on the effector side of the reflex arc (p. 59). This is the sense in which the term is applied by Sherrington in the following passage (Integrative Action of the Nervous System, p. 84):

"Reflex coördination makes separate muscles whose contractions act harmoniously, *e. g.*, on a lever, contract together, although at separate places, so that they assist toward the same end. In other words, it excites synergic muscles. But it in many cases does more than that. Where two muscles would antagonize each other's action the reflex arc, instead of activating merely one of the two, causes when it activates the

one depression of the activity (tonic or rhythmic contraction) of the other. The latter is an inhibitory effect."

The motor paths and centers in general are more simply organized than are the sensory paths and centers. The nervous discharges through these motor systems are very direct and rapid. Complex nervous reactions require more time than simple reflexes, and this delay or central pause is chiefly in the correlation centers rather than in the efferent coördination mechanisms (see pp. 71, 104, 199).

The word *association* may be reserved for those higher correlations where plasticity and modifiability are the dominant features of the response and whose centers are separated from the peripheral sensory apparatus by the lower correlation centers which are devoted to the stereotyped invariable reflex responses. Correlation may be mechanically determined by innate structure, or there may be some small measure of individual modifiability, but when the modifiability comes to be the dominant characteristic, so that the result of the stimulus cannot be readily predicted with mechanical precision, the process may be called association. The intelligent types of reaction and all higher rational processes belong here, and the cerebral cortex is the chief apparatus employed.

The boundaries between the three types of centers just distinguished are not always sharply drawn, especially in their simpler forms, though in general they are easily distinguished. The mechanisms of coördination are neurologically simpler than those of correlation and association, and in general they are developed in the more ventral parts of the brain and spinal cord, that is, below the limiting sulcus of the embryonic brain (p. 125). The correlation and association centers are developed in the more dorsal parts of the brain and cord, and the greater part of the thalamus and cerebral hemispheres is composed of tissue of this type. Nevertheless, the distinctions here drawn are fundamentally physiological rather than anatomical, and coördination centers may be developed in the dorsal parts of the brain, as in the case of the cerebellum and probably also the corpus striatum of mammals.

Integration is the combination of different nervous processes or reflexes so that they coöperate in a larger activity and thus unify the bodily functions. The process of integration is the highest function of the nervous system. In the primitive segmental nervous systems (p. 30) each segmental ganglion is the integrative center for its own segment, and the fusion of ganglia indicated in Figure 3 is effected in the interest of more complete integration of the activities of the body as a whole. In the evolution of the vertebrate type of nervous system there has been a similar progressive condensation of centers of integration in the brain. In lower vertebrates the isolated spinal cord can perform many functions which in man require the participation of the brain. See further on p. 68.

Summary.—The functions which characterize the nervous system have been derived from those of ordinary protoplasm by further development of three of the fundamental protoplasmic properties—viz., excitability, conductivity, and correlation. The most primitive form of nervous system known is diffuse and local in its action, but in all the more highly de-

veloped forms the chief nervous organs tend to be centralized for ease of general correlation and control. Most of the types of nervous systems found in the animal kingdom are represented in two distinct and divergent lines of evolution, one adapted especially well for the reflex and instinctive mode of life and found in the worms, insects, and their allies, and the other found in the vertebrates and culminating in the human brain with its remarkable capacity for individually acquired and conscious functions.

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CHAPTER III

THE NEURON

As we have seen in the last chapter, the functions of irritability, conduction, and correlation are the most distinctive features of the nervous system. Like the rest of the body, the nervous tissues are composed of cells, the irritability of whose protoplasm is of diverse sorts in adaptation to different functional requirements. Each sense organ, for instance, is irritable to its own adequate stimulus only (see pp. 26, 74). The functions of correlation and integration of bodily actions cannot be carried on by the nerve-cells as individuals, but they are effected by various types of connections between the different cells in the nerve-centers. The character of any particular correlation, in other words, is a function of the pattern in accordance with which the nerve-cells concerned are connected with each other and with the end-organs of the reflex arcs involved. The conducting function of nerve-cells is, perhaps, their most striking peculiarity, and their very special forms are due largely to the fact that their business is to connect remote parts of the body so that these parts can coöperate in complicated movements.

Not all of the cells which compose the central nervous system are nerve-cells. In addition to non-nervous connective tissue elements which grow into the central nervous system from without accompanying the blood-vessels, the substance of the brain and spinal cord contains a supporting framework composed of ependyma, neuroglia fibers and glia cells. These are not known to perform nervous functions, though nutritive and other functions have been ascribed to them (see p. 111 and the paper by Achucarro (1915).

The *ependyma* is the membrane which lines the ventricles of the brain and spinal cord. It is derived from the original epithelium of the embryonic neural tube (see pp. 114, 125) by a very complicated process (see Hardesty, 1904). This primary epithelium also gives rise to free cells which lie among the immature ependyma cells. These free cells are called germinative cells or indifferent cells. They rapidly increase by division and some of them ultimately transform into the nerve cells, while others become free neuroglia or glia cells. From the neuroglia

cells are formed numerous tough non-nervous filaments, the neuroglia fibers, which interlace to form a felt-work whose function seems to be merely the mechanical support of the brain substance.

The true nerve-cells are called *neurons*. There has been a long controversy regarding the way in which the neurons of the adult body are developed from the cells of the embryonic nervous system; but it is now generally accepted that each neuron is developed from a single embryonic cell (known as a neuroblast), and that in the adult body each neuron has a certain measure of anatomical and physiological distinctness from all of the others.

The very young nerve-cell (neuroblast) is oval in form and is composed of a nucleus and its surrounding protoplasm (cytoplasm); but in further development it rapidly elongates by the outgrowth of one or more fibrous processes from the cell body, so that the mature neuron may be regarded as a protoplasmic fiber with a thickening somewhere in its course which is the cell body of the original neuroblast and contains the cell nucleus and a part only of its cytoplasm (this part being called the perikaryon), the remainder of the cytoplasm composing the fibrous processes, that is, the nerve-fibers. The cell body of the mature neuron is sometimes loosely termed the nerve-cell, though the latter term should strictly include the entire neuron. The importance of the conducting function is reflected in the elongated forms of the neurons and in the peculiar protoplasmic structure of the nerve-fibers. The function of the cell body is chiefly nutritive; the entire neuron dies if the cell body is destroyed.

Each neuron may be regarded as essentially an elongated conductor, and these units are arranged in chains in such a way that a nervous impulse is passed from one to another in series. Since the arrangement is such that the nervous impulse usually passes through the series in only one direction (see the typical reflex arc, Fig. 1, p. 26), each neuron has a receptive function at one end and discharges its impulse at the other end. This is what is meant by the *polarity of the neuron* (see pp. 55, 103).

The simpler forms of neurons are bipolar, with one or more processes known as *dendrites* conducting nervous impulses

toward the cell body, and (usually) only one process, the *axon* or neurite, conducting away from the cell body. The den-

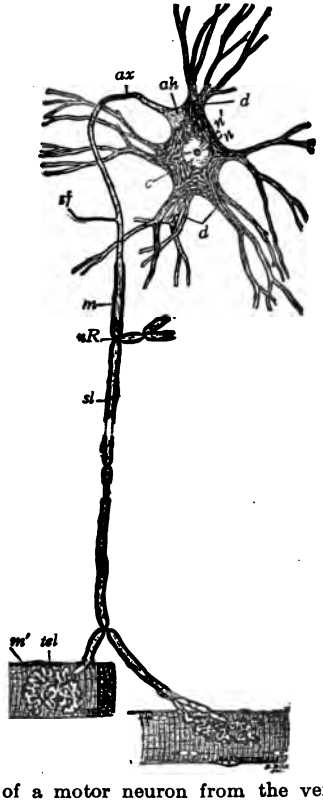

Fig. 5.—Diagram of a motor neuron from the ventral column of gray matter in the spinal cord. The cell body, dendrites, axon, collateral branches, and terminal arborizations in muscle are all seen to be parts of a single cell and together constitute the *neuron: ah*, axon hillock free from chromophilic bodies; *ax*, axon; *c*, cytoplasm of cell body containing chromophilic bodies, neurofibrils, and other constituents of protoplasm; *d*, dendrites; *m*, myelin (medullary) sheath; *m'*, striated muscle-fiber; *n*, nucleus; *n'*, nucleolus; *nR*, node of Ranvier where the axon divides; *sf*, collateral branch; *sl*, neurilemma (not a part of the neuron); *tel*, motor end-plate. (After Barker, from Bailey's Histology.)

drites are usually short, and in this case their structure is similar to that of the cell body. But where the dendrites

are long, as in the neurons of the spinal and cranial ganglia (Figs. 1, 10), they may have the same structure as the axon. The axons (and in the case of neurons of the spinal and cranial ganglia the dendrites also) are the axis-cylinders of the longer nerve-fibers and are structurally very different from the protoplasm of the cell body, being composed chiefly of numerous very delicate longitudinally arranged neurofibrillæ embedded in a small amount of more fluid protoplasm. The

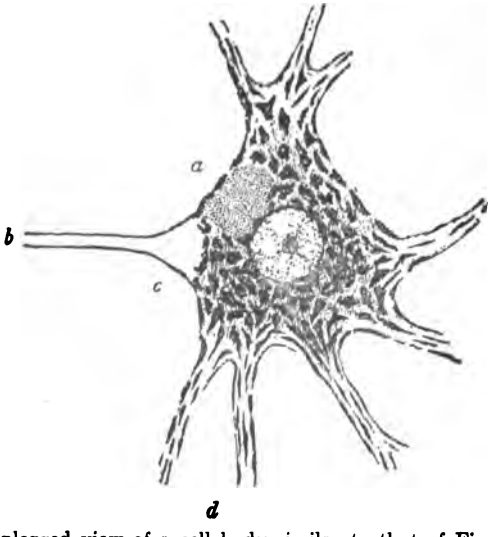

Fig. 6.—Enlarged view of a cell body similar to that of Fig. 5, from the spinal cord of an ox, showing the large chromophilic bodies: *a*, Pigment; *b*, axon; *c*, axon hillock; *d*, dendrites. (After von Lenhossék.)

axon usually arises from the cell body; it may arise from the base of one of the dendrites or, rarely, from the apex of the chief dendrite (Fig. 11).

The forms of neurons are infinitely diverse and appear to have been determined by two chief factors; these are (1) the nutrition of the cell and (2) the specific functions of conduction to be served. The dendrites spread widely throughout the surrounding tissues, thus giving the cell a large surface for the rapid absorption of food materials from the surrounding

lymph. This was regarded as the only function of the dendrites by Golgi and some of the other pioneers in the study of neurons, and led them to apply the name "protoplasmic processes" to these structures. We have already seen that the dendrites are more than this, however, being the usual avenues by which nervous impulses enter the cell body. The size, length, and mode of branching of the dendrites are, therefore, chiefly determined by their relations to other neurons from

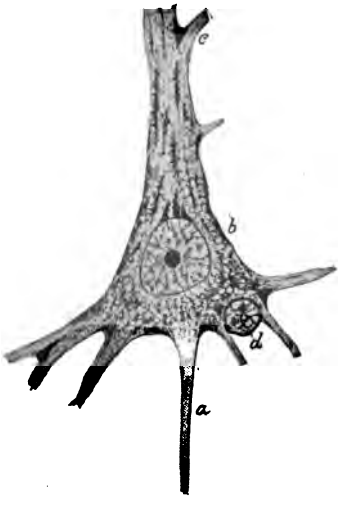

Fig. 7.—The body of a pyramidal neuron from the cerebral cortex, stained by Nissl's method, illustrating the arrangement of the chromophilic substance and the form of the nucleus: *a*, axon; *b*, chromophilic bodies surrounding the nucleus; *c*, a mass of chromophilic substance in the angle formed by the branching of a dendrite; *d*, nucleus of a neuroglia cell (not a part of the neuron). (After Ramón y Cajal.)

which they receive their nervous impulses. The axon probably plays but little part in the general nutrition of the cell, and its form is shaped almost entirely by the distance to be traversed in order to reach the center or centers into which it discharges.

Neurons can function only when connected together in chains, so that the nervous impulse can be passed from one to the other. In any such chain the neuron first to be excited

is called the neuron of the first order, and the succeeding members of the series neurons of the second, third, fourth order, and so forth. All reflexes require an afferent neuron which conducts the nervous impulse from the receptor to the center, one or more efferent neurons conducting from the center to the organ of response, and usually one or more neurons intercalated between these within the center itself (see pp. 26, 59, 117). Figure 1, p. 26, illustrates the simplest possible connection of neurons in a reflex arc of the spinal cord, involving only two elements. The afferent neuron sends its dendrite to the skin and its axon into the spinal cord, where the nervous impulse is taken up by the dendrites of the efferent neuron, which in turn transmits it to a muscle. Figures 5 to 9 illustrate the forms of other neurons.

The different dendrites of a neuron may be physiologically all alike, or they may spread out in different directions to receive nervous impulses of diverse sorts from different sources. Similarly the axon may discharge its nervous impulse into a single nerve center or peripheral end-organ, or it may branch, thus connecting with and stimulating to activity two or more diverse functional mechanisms. In other words, a given neuron may be a link in a chain of some simple nervous circuit (Fig. 1), or it may be adapted to collect nervous impulses from different sources and discharge them into a single final common path, or in the third place it may receive nervous impulses of one or more functional sorts and then discharge its own nervous energy into several remote parts of the nervous system. This, in brief, is the mechanism of correlation, and illustrations of these different types of connection will be found in the following chapters. If animal reactions were simple responses so arranged that a given stimulus could produce only one kind of movement, the only nervous mechanism required would be a single neuron transmitting the excitation from the point of stimulation to the organ of response, as a call bell may be rung by pulling a bell cord. But the actual reactions are always more complex than this, so that several neurons must be connected in series with various divergent pathways of nervous discharge which reach different correlation centers, all of which must coöperate in the final

response. Illustrations of some of these complicated reflex mechanisms will be found in Chapter IV.

Fig. 8.—Pyramidal neuron (Type 1 of Golgi) from the cerebral cortex of a rabbit. The axon gives off numerous collateral branches close to the cell body and then enters the white substance, within which it extends for a long distance. Only a small part of the axon is included in the drawing: *a*, axon; *b*, white substance; *c*, collateral branches of axon; *d*, chief dendrite; *p*, its terminal branches at the outer surface of brain. (After Ramón y Cajal.)

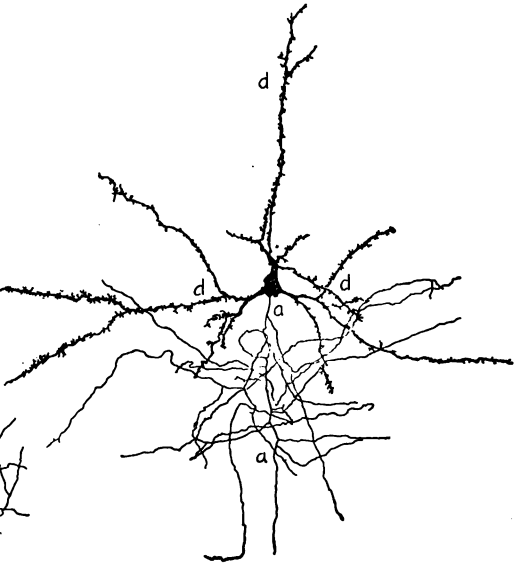

Fig. 9.—Neuron of Type II from the cerebral cortex of a cat. The entire neuron is included in the drawing: *a*, axon which branches freely and terminates close to the cell body; *d*, dendrites. (After Kölliker.)

Neurons with short dendrites and a single long axon are the most common form and were termed Type I by Golgi (Fig. 8).

In some cases (Fig. 9) the axon also is very short, breaking up in the immediate neighborhood of the cell body; these are the Type II neurons of Golgi and appear to be adapted for the diffusion and summation of stimuli within a nerve center. The neurons of the spinal and cranial ganglia form a third type. In embryonic development they begin as bipolar cells with a dendritic process at one end and an axonal process at the opposite end of the cell body; but in the course of further development (Fig. 10) the two processes approach each other and finally unite for a short distance into a single stem, which then separates into an axon and a highly special form of dendrite which has the same microscopic structure as the axon, but con-

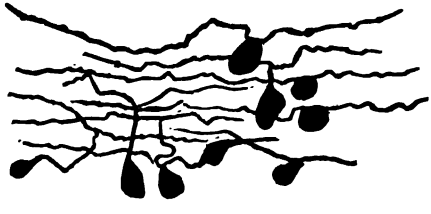

Fig. 10.—A collection of cells from the ganglion of the trigeminus of the embryonic guinea-pig, to illustrate various stages in the transformation of bipolar neuroblasts into unipolar ganglion cells. (After Van Gehuchten.)

ducts in the opposite direction with reference to the cell body. This produces a T-form unipolar cell.

The peculiarities of the neurons of the spinal and cranial ganglia (Figs. 1 and 10) have given rise to much discussion. Many neurologists consider that these neurons have two axons and no dendrites because of the structural similarity of their two chief processes. Dogiel, however, has described many different types of neurons in the spinal ganglia, some of which have short dendrites of the more typical form. Lugaro has shown that the neurons of the spinal ganglia suffer chromatolysis (see p. 50) when the peripheral process is cut off from the cell body but not when the central process is similarly severed. This has also been used as an argument against regarding the peripheral process as a dendrite (see A. Meyer in Jour. Comp. Neurology, vol. viii, 1898, pp. 265–267). But to avoid confusing different points of view, it seems better to define dendrite and axon in terms of a single criterion, viz., the functional polarization or direction of conduction with reference to the cell body, as on page 40.

Neurons differ in internal structure, as well as in form, from the other cells of the body. The most important of these pecu-

liarities are, first, the fibrillar structure of their cytoplasm, and, second, the presence in the cytoplasm of a highly complex protein substance chemically allied to the chromatin, which is the best known and probably the most important constituent of the cell nucleus. This is the *chromophilic substance*, which in nerve-cells as seen under the microscope is ordinarily arranged in more or less definite flake-like masses scattered throughout the cytoplasm of the cell and extending out into the larger dendrites (see Figs. 6, 7). These masses were first carefully investigated by Nissl, who devised a special staining method for that purpose; they are, accordingly, often called the Nissl bodies,

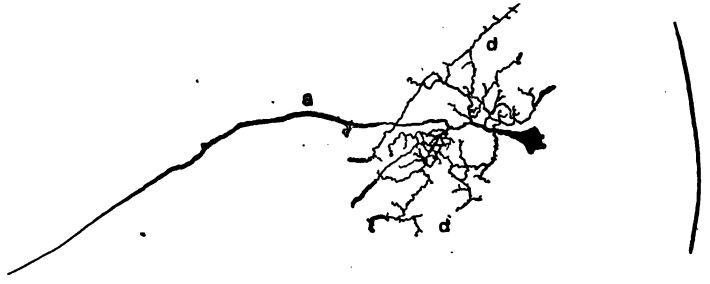

Fig. 11.—A neuron from the primary gustatory center in the medulla oblongata of the carp. (Figure 139 (2), p. 340, illustrates the enormous enlargement of the medulla oblongata of this fish which is produced by this gustatory center.) The peripheral gustatory nerves end among the dendrites, *d*. The axis of the main dendrite is directly prolonged to form the axon, *a*. The heavy line at the right marks the external surface of the brain. (From the Journal of Comparative Neurology, vol. xv, p. 395.)

and sometimes tigroid bodies. They never occur in the axon nor in a special conical protuberance of the cell body (the axon hillock) from which the axon arises (see Fig. 5, *ah*, and Fig. 6, *c*).

It is becoming increasingly probable that the chromophilic substance in the living neuron is diffused throughout the protoplasm and that the definite granules (Nissl bodies) seen in stained preparations are fixation artefacts produced by the coagulation of this substance and its precipitation by the action of the reagents employed. It remains true, however, that functionally different kinds of neurons usually

exhibit, when fixed and stained for microscopic study, characteristic arrangements of the chromophilic granules. In fact, the limits of different functional centers in the brain can often

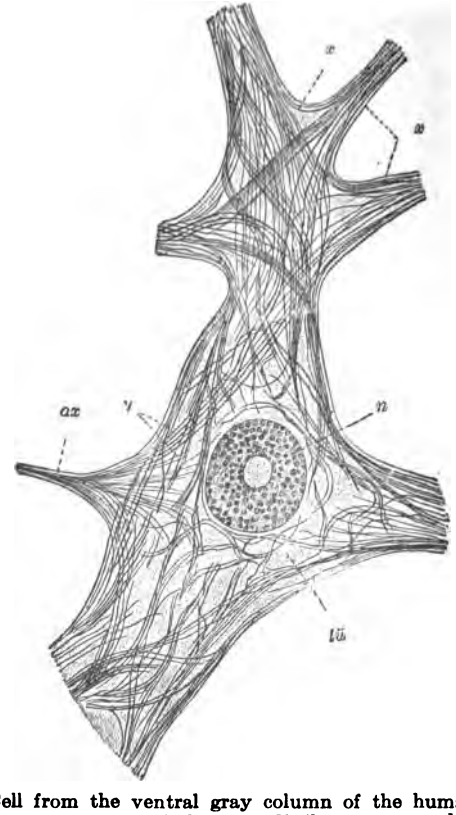

Fig. 12.—Cell from the ventral gray column of the human spinal cord, illustrating the arrangement of the neurofibrils: *ax*, axon; *lü*, interfibrillar spaces occupied by chromophilic substance; *n*, nucleus; *x*, neurofibrils passing from one dendrite to another; *y*, similar neurofibrils passing through the body of the cell. (After Bethe, from Heidenhain's Plasma und Zelle.)

be determined by this criterion alone, that is, by the abundance, size, and arrangement of the Nissl bodies as contrasted with the neurons of surrounding regions with different functions.

The neurofibrils are very delicate strands of denser protoplasm found in all parts of the neuron except the nucleus. They are by many regarded as the specific conducting elements of the neuron, though the evidence for this is not conclusive. They ramify throughout the cytoplasm (Fig. 12), passing through the cell body from one process to another.

Mitochondria.—Nerve-cells, in common with most other animal and plant cells, possess in all parts of their protoplasm except the nucleus very small granules known as mitochondria and possessing specific staining properties. Their occurrence in nerve cells has been carefully investigated by Cowdry. Their sizes and shapes vary in different kinds of cells and in the same cell at different times. These granules seem to be fundamental ingredients of nearly all protoplasm and are probably concerned in the most fundamental protoplasmic activities. Unlike the chromophilic substance, they do not show obvious changes when the nerve-cells are greatly fatigued and their precise function remains obscure. Still other kinds of granules are known to occur in nerve-cells, about which our knowledge is even more imperfect.

The longer nerve-fibers are usually enveloped by a thick white glistening sheath of myelin, a fat-like substance. This *myelin sheath*, or medullary sheath, is usually regarded as a part of the neuron with which it is related and the fibers which possess it are called myelinated or medullated fibers; these fibers compose the white matter of the brain and a large part of the peripheral nerves (see Fig. 5). There may be, in addition, in the case of the peripheral nerves an outer sheath, the *neurilemma* (primitive sheath or sheath of Schwann). This is a thinner nucleated membrane, not a part of the neuron to which it is attached, but formed from surrounding cells.

Nemiloff (1910) describes the myelin sheath of peripheral nerves as quite separate from the axis cylinder, but on the other hand very intimately related with the nuclei of the neurilemma sheath of the ordinary descriptions. But these nuclei he thinks are related, not to the neurilemma sheath, but to a spongy protoplasmic network which spreads throughout the myelin sheath and has heretofore been described as the neurokeratin network. Neither the neurilemma nor the myelin sheath, on this view, could be regarded as parts of the neuron; but, with the contained protoplasmic network and nuclei, these are added to the axis cylinder from the surrounding cells during the development of the fiber. This description applies only to the peripheral nerves. Nerves within the central nervous system may possess myelin sheaths but no well-formed neurilemma or nuclei. It is therefore difficult to understand how Nemiloff's description can apply to these fibers, and this matter evidently requires further investigation.

The function of the myelin sheath has often been regarded as simply that of an insulating substance to prevent the overflow and loss of the nervous impulse conducted by the axon, but there is some evidence that this sheath plays an important part in the chemical processes involved in the act of nervous conduction. The neurilemma is likewise often spoken of as a protecting membrane. Whether it has any other function in the normal life of the nerve-fiber is unknown; but if a nerve-fiber is by accident severed from its cell body, it is known that the nuclei of the neurilemma play a very important part in the degeneration and regeneration of the severed fiber and the restoration of its normal function.

As has been suggested, nerve-fibers cut off from their cell bodies immediately die and degenerate. But in the case of peripheral nerves the neurilemma nuclei do not die; and, apparently with the aid of these nuclei, a new nerve-fiber may under favorable conditions grow out from the central stump of the cut nerve, and finally the entire nerve may regenerate. In the central nervous system, where the neurilemma is absent or greatly reduced, the regeneration of such injured nerves takes place with great difficulty, if at all.

It is possible by a special method of staining devised by Marchi to differentiate myelinated fibers which are in process of degeneration from the normal fibers with which they may be mingled. This method has often permitted a much more precise determination of the exact course of the fibers of a given peripheral nerve or central tract than would be possible by the examination of normal material, especially after experimental operations on the lower animals, where the particular collection of fibers under investigation may be severed and then later the animal killed and examined by Marchi's method (see p. 145).

It is also found that after cutting any group of nerve-fibers the cell bodies from which these fibers arise show structural changes. The most important change is a solution of the chromophilic substance or Nissl bodies so that they no longer appear in a stained preparation (Fig. 13). This is termed *chromatolysis*, and often enables the neurologist to determine

exactly which cells in the central nervous sytem give rise to a particular bundle of fibers (for examples see pp. 147 and 318).

The neuron doctrine may be said to date from the publication of important papers by Golgi, of Pavia, in 1882 to 1885 (though his now famous method was published in 1873, and many of Golgi's theoretical conclusions have been greatly

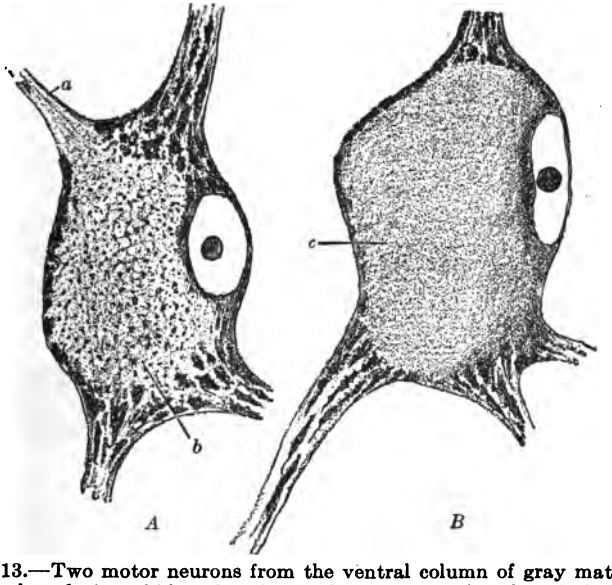

Fig. 13.—Two motor neurons from the ventral column of gray matter of the spinal cord of a rabbit, taken fifteen days after cutting the sciatic nerve, to illustrate the chromatolysis of the chromophilic substance: *A*, cell in which the chromophilic bodies are partially disintegrated (at *b*) and the nucleus eccentric; *B*, cell showing more advanced chromatolysis (*c*), the chromophilic substance being present only in the dendrites and around the nucleus in the form of a homogeneous mass; *a*, axon. Compare with these appearances the normal cell of the ventral column shown in Fig. 6. (After Ramón y Cajal.)

modified). The name *Neuron* (in English often spelled "neurone") was first applied by Waldeyer in 1891 in connection with a clear enunciation of the recently demonstrated facts upon which the concept is based. The discovery of William His that the nervous system is made up of cellular units which are embryologically distinct, and the further

demonstration by others that these cellular elements retain some measure of anatomical and physiological individuality (the exact degree of anatomical separation is still in controversy—some say it is complete) up to adult life revolutionized neurology, and this doctrine has profoundly influenced all subsequent neurological work. The history of this move-

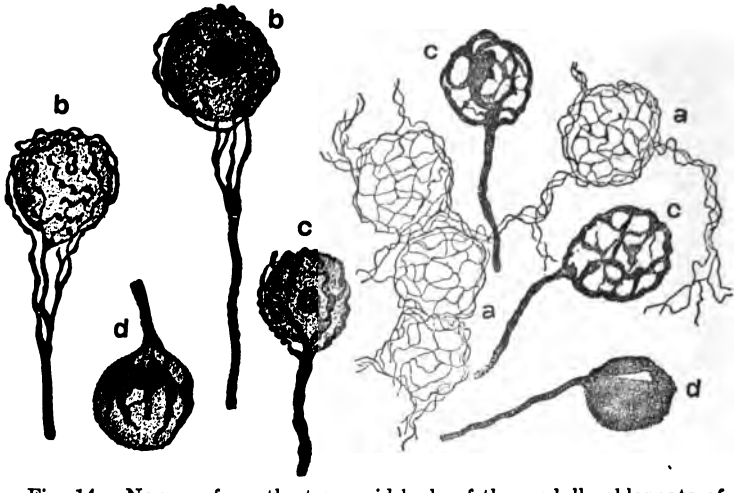

Fig. 14.—Neurons from the trapezoid body of the medulla oblongata of a cat, illustrating different forms of synapse: *a*, Delicate pericellular net around the cell body of a neuron which is not shown; *b*, coarser endings; *c*, still coarser net; *d*, calyx-like envelope. In *b*, *c*, and *d*, at the left of the figure, the globular cell body of the neuron of the second order is shaded with lighter stipple than the terminals of the axon of the neuron of the first order. (After Veratti, from Edinger's Vorlesungen.) (It should be noted that in this account we do not follow Veratti's interpretations of these structures, but that of Held, Ramón y Cajal, and the majority of other neurologists.)

ment we cannot here go into (see the excellent summaries in Barker's Nervous System and the article by Adolf Meyer cited at the end of this chapter). The present status of the neuron doctrine has been summarized by Heidenhain (1911, p. 711) in the following six propositions:

1. The neuron of the adult animal body is an anatomical unit; it corresponds morphologically to one cell.

2. The neuron is, accordingly, also a genetic unit, for it is differentiated from a single embryonic cell.

3. Nervous substance is composed of the contained neurons; within the nervous system there are no elements other than neurons which participate in nervous functions.

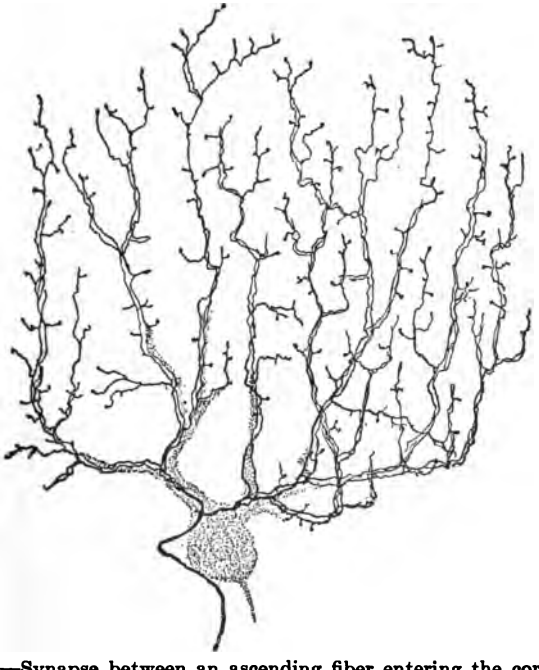

Fig. 15.—Synapse between an ascending fiber entering the cortex of the cerebellum and the dendrites of a Purkinje cell. (After Ramón y Cajal.)

4. The neurons remain anatomically separate; they are merely in contact with each other, that is, there are no connections between them which are characterized as conditions of continuity or fusion of their substance.

5. The neuron is a trophic unit. This means that the injury of any part of the neuron affects the welfare of the whole, and the destruction of the nucleus and cell body destroys the entire neuron, but such injuries do not directly affect adjacent neurons.

6. The neuron is a functional unit or, better, *the* functional unit of the nervous system.

These six propositions are accepted in their entirety by many neurologists; but it should be clearly understood that all of them are controverted by others. The fourth proposition, in particular, has been the subject of violent attack (see the discussion of the synapse below). The neuron, moreover, is a functional unit (proposition 6) in only a rather limited sense (see p. 59). Without further discussion of the merits of these controversial questions, it may be regarded as generally accepted that all of the preceding propositions have some measure of factual basis, though different neurologists would give various interpretations and modifications of some of them.

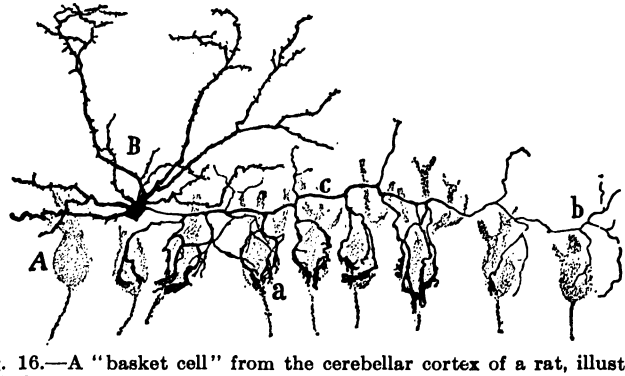

Fig. 16.—A "basket cell" from the cerebellar cortex of a rat, illustrating the discharge of a single neuron, *B*, by synaptic connection with the cell bodies of several Purkinje neurons, *A*, by basket-like endings of the axon: *A*, cells of Purkinje; *a*, the basket-like synapse on the body of a Purkinje cell; *B*, the basket cell; *b*, terminus of the axon; *c*, axon of basket cell. (After Ramón y Cajal; cf. Fig. 89, p. 214.)

The place where the axon of one neuron comes into physiological relation with another neuron is known as the *synapse*. Its precise nature is still obscure. Structurally it usually exhibits a dense interlacing of the terminal arborization of an axon of one neuron with the bushy dendrite of a second neuron. In Fig. 1 (p. 26) such a synapse is seen between the dorsal root neuron and the ventral root neuron. In other cases the terminal arborization takes the form of a delicate network

which twines around the cell body of the second neuron or of a calyx-like expansion or coarse-meshed reticulum closely enveloping the cell body (Fig. 14). Another form of synapse is seen in Fig. 15 from the cortex of the cerebellum. The body and larger dendrites of a single cortical neuron of the type known as Purkinje cells (see p. 215) are shown in gray, and the terminal branches of an afferent neuron are seen twining about the dendritic branches of the Purkinje cell, thus forming a very intimate union. Similar synapses are found in the cerebral cortex (p. 305). Figure 16 illustrates a type of synapse also found in the cerebellar cortex. A single "basket cell," *B*, has a short axon whose branches form synapses around the bodies of a large number of Purkinje cells, thus diffusing and greatly strengthening the nervous discharge (see p. 216 and Fig. 89, *b*). For still other types of synapse see Figs. 61, 89, 98, 104, 109, 126.

The synapse has been a crucial point in recent discussions regarding the general physiology of the nervous system, many neurologists believing that it is the most important part of the reflex circuits (see, for instance, on the theory of sleep, p. 110). The doctrine of the polarization of the neuron (p. 40) implies that at the synapse there must be a reversal of the polarity with reference to the cell body as the nervous impulse passes over from an axon to a dendrite.

In the simple diffuse form of nervous system found in primitive animals like the jelly-fishes and lowest worms (p. 29) the nerve-cells are described as connected by protoplasmic strands to form a continuous network. Here, of course, there are no synapses and the neurons are not polarized. Apparently the nervous impulse may be transmitted equally well in all directions throughout this network. The physiological properties of such an arrangement appear to be very different from those of the synaptic nervous systems of higher animals. A non-synaptic network similar to that mentioned above has been described as occurring in some of the diffuse ganglionic plexuses of the human body (Fig. 17).

In the synaptic systems, as found in all highly differentiated nervous centers, the majority of neurologists teach that at the synapse the two neurons involved are simply in contact and that the nervous impulse passes from one to the other across a

very short gap in the conducting substance. Others believe that they have demonstrated very delicate protoplasmic threads which bridge this gap, thus establishing continuity of the conducting substance across the synapse. Good histological preparations show, however, in some of the most intimate synapses known where the axon ends directly on the cell body

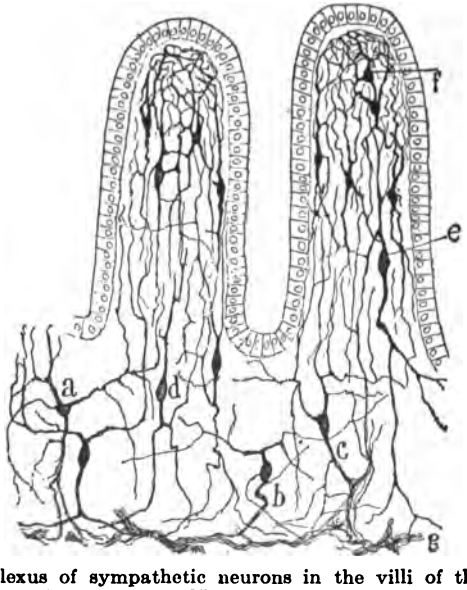

Fig. 17.—Plexus of sympathetic neurons in the villi of the small intestine of a guinea-pig: *a*, *b*, *c*, *d*, Neurons of the subepithelial plexus; *e*, *f*, neurons of the plexus within the villi; *g*, fibers of the submucous (Meissner's) plexus. (After Ramón y Cajal.)

of the second neuron that there is a distinct membranous cell wall around the terminals of the fibers of the first order and a second membrane enveloping the body of the neuron of the second order, so that continuity of the ordinary protoplasm of the neurons here seems to be quite impossible, so far as our present technic is adequate to decide the question.[1]

[1] For an illustration of such a synapse see BARTELMEZ, G. W., Mauthner's Cell and the Nucleus Motorius Tegmenti, Jour. Comp. Neur., vol. xxv, 1915, Figs. 11, 12, and 13, pp. 126–128; and the Morphology of the Synapse in Vertebrates, Archives of Neurology and Psychiatry, Chicago, vol. iv, 1920, pp. 122–126.

The following important points regarding the synapse seem to be established:

1. Unimpeded protoplasmic continuity across the synapse has not been clearly established, and in some cases there is clearly a membranous barrier interposed between the two neurons. But the exact nature of this barrier is unknown and it by no means follows that the synaptic membrane is an inert substance. It may be composed of living substance of a different nature from that of the other protoplasm of the neurons.

2. The transmission of the nervous impulse across the synapse involves a delay greater than that found in the nerve-fiber or the cell body. This suggests that there is some sort of an obstruction here which does not occur elsewhere in the reflex arc (see p. 104).

3. The synapse is more susceptible to certain toxic substances, such as nicotin, than is any other part of the reflex arc.

4. Though a nerve-fiber seems to be capable of transmitting an impulse in either direction, the nervous impulse can pass the synapse in only one direction, viz., the direction of normal discharge from the axon of one neuron to the dendrite of another. The synapse, therefore, acts as a sort of valve, to use a crude analogy, and appears to be one of the factors (not necessarily the only one, see p. 103) in establishing the polarity of the neuron.

5. Observations upon injured neurons show that the degenerations caused by the severance of their fibrous processes (whether these be manifested as degeneration of the fibers or as chromatolysis, see p. 50) or by the destruction of the cell bodies from which the fibers arise cannot cross the barriers interposed by the synapses.

Summary.—In this chapter the form and internal structure of neurons have been briefly reviewed and the present status of the neuron doctrine is summarized on p. 52. The synapse is the place where the nervous impulse is transmitted from one neuron to another, and it is regarded as of the utmost physiological importance, its most important features being presented briefly on this page, above. The doctrine of the polarization of the neuron teaches that nervous impulses are received by

the dendritic processes and transmitted outward from the cell body through the axon.

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CHAPTER IV

THE REFLEX CIRCUITS

THE cellular unit of the nervous system, as we have seen, is the neuron. Neurons, however, never function independently, but only when joined together in chains whose connections are correlated with the functions which they serve. Accordingly, the most important unit of the nervous system, from the physiological standpoint, is not the neuron, but the *reflex circuit*, a chain of neurons consisting of a receptor or sensory organ, a correlating center or adjustor, and an effector or organ of response, together with afferent and efferent nerve-fibers which serve as conductors between the center and the receptor and effector respectively (see p. 26). In a reflex circuit the parts must be so connected that upon stimulation of the receptive end-organ a useful or adaptive response follows, such, for instance, as the immediate jerking away of the hand upon accidentally touching a hot stove.

A *reflex act*, as this term is usually defined by the physiologists, is an invariable mechanically determined adaptive response to the stimulation of a sense organ, involving the use of a center of correlation and the conductors necessary to connect this center with the appropriate receptor and effector apparatus. The act is not voluntarily performed, though one may become aware of the reaction during or after its performance.

The term "reflex" is often popularly very loosely applied, but as generally used by physiologists it involves the rather complex nervous function above described. If an electric shock is applied directly to a muscle or to the motor nerve which innervates that muscle, the muscle will contract, but this direct contraction is not a reflex act. Many acquired movements have become so habitual as to be performed quite automatically, such as the play of the fingers of an expert pianist or typist; but these *acquired automatisms* must be

clearly distinguished from the reflexes, which belong to the innate nervous organization with which we are endowed at birth (see pp. 33, 338). The lowly organisms which lack a differentiated nervous system exhibit many kinds of behavior which closely resemble reflexes and, in fact, are physiologically of the same type; but these non-nervous responses are usually termed tropisms or taxes, though some physiologists call them reflexes, and some reflexes, as above defined, are often called tropisms.

The structure of the simple reflex circuit is diagrammatically illustrated in Fig. 18, A. The receptor (*R*) may be a simple terminal expansion of the sensory nerve-fiber or a very complex sense organ. The effector (*E*) may be a muscle or a gland. The cell body of the afferent neuron (1) may lie within the center (*C*) or outside, as in the diagram. The latter condition is more usual, as seen in the spinal and cranial ganglia (Fig. 1, p. 26). The synapse and the cell body of the efferent neuron (2) lie in the center.

A simple reflex act involving the use of so elementary a mechanism as has just been described is probably never performed by any adult vertebrate. The nervous impulse somewhere in its course always comes into relation with other reflex paths, and in this way complications in the response are introduced. Some illustrations of the simpler types of such complex reflex circuits will next be considered.

Separate reflex circuits may be so compounded as to give the so-called chain reflex (Fig. 18, B). Here the response of the first reflex serves as the stimulus for the second, and so on in series. The units of these chain reflexes are usually not simple reflexes as diagrammed, but complex elements of the types next to be described.

Figure 18, C illustrates another method of compounding reflexes so that the stimulation of a single sense organ may excite either or both of two responses. If the two effectors, *E*1 and *E*2, can coöperate in the performance of an adaptive response, the case is similar to that of Fig. 18, A, with the possibility of a more complex type of reaction. This is an allied reflex. If, however, the two effectors produce antagonistic movements, so that both cannot act at the same time, the result is a physiological dilemma. Either no reaction at all results, or there is a

sort of physiological resolution (sometimes called physiological choice), one motor pathway being taken to the exclusion of the other. Which path will be chosen in a given case may be determined by the physiological state of the organs. If, for

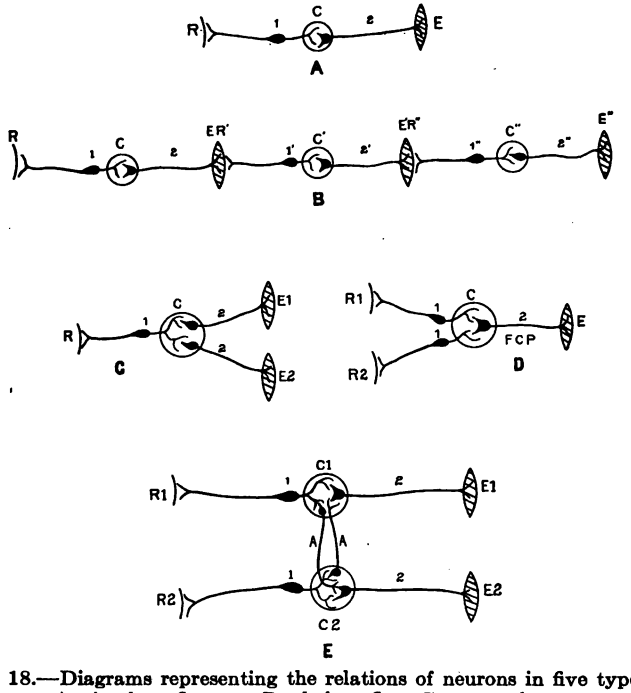

Fig. 18.—Diagrams representing the relations of neurons in five types of reflex arcs: A, simple reflex arc; B, chain reflex; C, a complex system illustrating allied and antagonistic reflexes and physiological resolution; D, a complex system illustrating allied and antagonistic reflexes with a final common path; E, a complex system illustrating the mechanism of physiological association. *A*, *A*, association neurons; *C*, *C'*, *C''*, *C*1, and *C*2, centers (adjustors); *E*, *E'*, *E''*, *E*1, and *E*2, effectors; *FCP*, final common path; *R*, *R'*, *R''*, *R*1, and *R*2, receptors.

instance, one motor system, *E*2, is greatly fatigued and the other rested, the threshold of *E*2 will be raised and the motor discharge will pass to *E*1.

Figure 18, D illustrates the converse case, where two receptors discharge into a single center, which, in turn, by means of a final common path (*FCP*) excites a single effector (*E*). If the

two receptors upon stimulation normally call forth the same response, they will reinforce each other if simultaneously stimulated, the response will be strengthened, and we have another type of allied reflex. But there are cases in which the stimulation of *R*1 and *R*2 (Fig. 18, D) would naturally call forth antagonistic reflexes. Here, if they are simultaneously stimulated, a physiological dilemma will again arise which can be resolved only by one or the other afferent system getting control of the final common path.

Figure 18, E illustrates still another form of combination of reflexes. Here there are connecting tracts (*A*, *A*) between the two centers so arranged that stimulation of either of the two receptors (*R*1 and *R*2) may call forth a response in either one of two effectors (*E*1 and *E*2). These responses may be allied or antagonistic, and much more complicated reflexes are here possible than in any of the preceding cases.

A few illustrations of the practical operation of these types of reflex circuits will be given here and many other cases are cited throughout the following discussions. A case of a simple reflex has already been mentioned in the sudden twitch of the hand in response to a painful stimulation of the skin. The simplest possible mechanism of this reaction involving only two neurons is shown in Fig. 1 (p. 26). In actual practice, however, the arrangement figured is one element only of a more complex reaction (see p. 63). Figure 19 illustrates a more usual form of this type of reaction, where a series of three or more neurons is involved and at least two cerebral centers. An auditory impulse coming to the brain from the ear through the VIII cranial nerve terminates in a primary acoustic center in the superior olive (a deep nucleus of the medulla oblongata, see p. 227), where it is taken up by an intercalary neuron of the second order and transmitted to the nucleus of the VI nerve. The result is a contraction of the external rectus muscle of the eyeball, turning the eye toward the side from which the auditory stimulus was received. So far as this reaction alone is concerned, it is a simple reflex, but in practice the external rectus muscle of one eye is never contracted apart from the other five muscles of that eye and all six muscles of the other eye. In this way alone can conjugate movements of the two eyes be effected for the accurate fixation of the gaze upon any object.

The entire system of conjugate movements is also entirely reflex and it is effected by an exceedingly complicated arrangement of nerve tracts and centers, of which the superior olive and the nucleus of the VI nerve are integral parts.

The chain reflex (see Fig. 18, B) is a very common and a very important type. Most of the ordinary acts in the routine of daily life employ it in one form or another, the completion of one stage of the process serving as the stimulus for the initiation of the next.

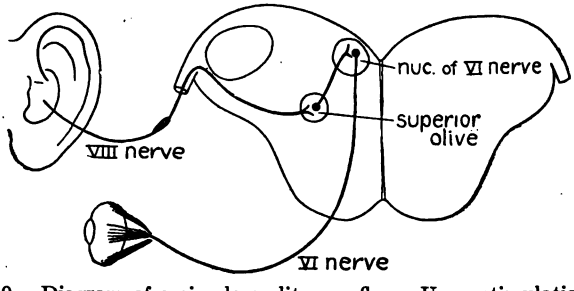

Fig. 19.—Diagram of a simple auditory reflex. Upon stimulation of the endings of the VIII nerve in the ear by sound waves, a nervous impulse may pass to the superior olive, whence it is carried by an intercalary neuron of the second order to the nucleus of the VI nerve. The fibers of this nerve end on the external rectus muscle of the eyeball.

There are within the muscles elaborate sense organs (the muscle spindles and their associated afferent nerves, see p. 92), which are stimulated by the contraction of the muscle. These afferent nerves of the muscle sense have their own centers of adjustment within the central nervous system, from which in turn efferent impulses go out which ultimately reach the same muscles from which the sensory impulses came in. This, of course, is a variety of chain reflex, and is the mechanism by which refined movements of precision are executed, where different sets of muscles must work against each other in constantly varying relations without conscious control. In the case of a sustained reflex series of this character this return flow of afferent impulses of the muscle sense, tendon sense, etc., exerts a constant influence upon the center which receives the initial stimulus, so that this center is constantly under the combined influence of the external stimulus which sets the reflex in motion and the internal stimuli arising from the

muscles themselves (proprioceptors, see p. 92) which control its course. In this case there is a true physiological circuit rather than an arc or segment of a circuit, as is commonly implied in the expression "reflex arc." This case is typical of the complex reflexes of the body in general, and for this and other considerations we follow the usage of Dewey (1893) and term the mechanism of a complete reflex a "reflex circuit" rather than an arc (see C. J. Herrick, 1913, and p. 345).

It has been suggested by Loeb also that many instincts are simply complex chain reflexes. Even in animals whose behavior is so complex as birds, a careful analysis of the cycle of nest building and rearing of young reveals many clear illustrations of this principle (see the works of F. H. Herrick, cited at the end of this chapter). Each step in the cycle is a necessary antecedent to the next, and if the series is interrupted it is often necessary for the birds to go back to the beginning of the cycle. They cannot make an intelligent adjustment midway of the series. This, of course, is not universally true. In birds, as in men, some measure of intelligent adjustment of the fixed instinctive cycles is often possible (see Craig in Biological Bulletin, vol. xxxiv, 1918, p. 105), but these two components of the behavior must not be confused.

The complex circuit illustrated by Fig. 18, C presents two possible types of reaction, either allied or antagonistic reflexes. The former case is illustrated again by the sudden movement of the hand in response to a painful stimulation of the skin. This is brought about, as we saw in considering the simple reflex, by a contraction of the arm muscles. But the muscles which move the elbow-joint are not, when the arm is at rest, entirely flaccid. Both flexors and extensors are always contracted to a certain degree, one balanced against the other. Now at the same time that the sensory stimulus from *R* (see Fig. 18, C) causes the contraction of the flexor muscle, *E*1, it also causes the relaxation of the antagonistic extensor, *E*2, the two efferent impulses coöperating to effect the avoiding reaction as rapidly as possible. In the antagonistic reflexes of our third type the physiological resolution involved in the selection of one or the other possible reaction always involves a delay in the response until one motor pathway dominates the system to the exclusion of the other.

In the fourth type of complex reflexes (see Fig. 18, D) two different sensory paths discharge into a single center, from which a final common path goes out to the effector. This mechanism also provides for both allied and antagonistic reflexes. A very simple apparatus for this type of reflex is found in the roof of the midbrain of the lowly amphibian, the common mud puppy, Necturus. Here the upper part of the midbrain roof receives optic fibers from the optic tracts, while the lower part receives fibers from the primary acoustic and tactile centers

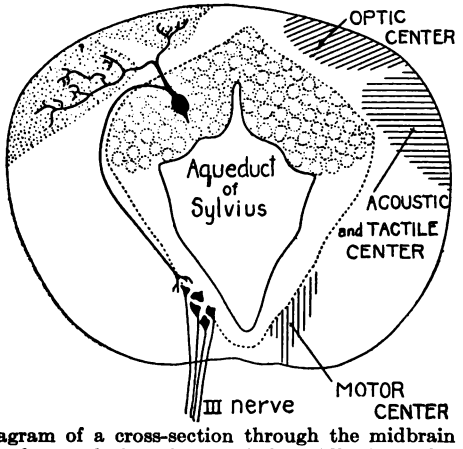

Fig. 20.—Diagram of a cross-section through the midbrain of Necturus, illustrating a single correlation neuron of the midbrain roof. One dendrite spreads out in the optic center among terminals of the optic tracts; another dendrite similarly spreads out in the acoustic and tactile center. The axon descends to connect with the motor neurons of the III nerve. For the details of this apparatus see Herrick (1917).

(Fig. 20). A single neuron of the midbrain may send one dendrite downward to receive acoustic or tactile stimuli (or both of these), and another dendrite upward to receive optic stimuli. If the animal receives visual and auditory stimuli simultaneously, the intercalary neuron of the midbrain may be excited by both sets of stimuli. Its discharge through the axon to the motor organs of response (say to the eye muscles by way of the III nerve, as in Fig. 20) will be the physiological resultant of both sets of excitations. If they reinforce each

other, the discharge will be stronger and more rapid; if, on the other hand, they tend to produce antagonistic responses, there will be an inhibition of the response or a delay until one or the other stimulus obtains the mastery.

Yerkes has given a striking illustration of this method of reinforcement of stimuli in his experiments on the sense of hearing in frogs. The reflex mechanism of touch, hearing, and vision in the midbrain of the frog is similar to that of Necturus as described above (Fig. 20). Yerkes found that frogs under laboratory conditions do not ordinarily react at all to sounds

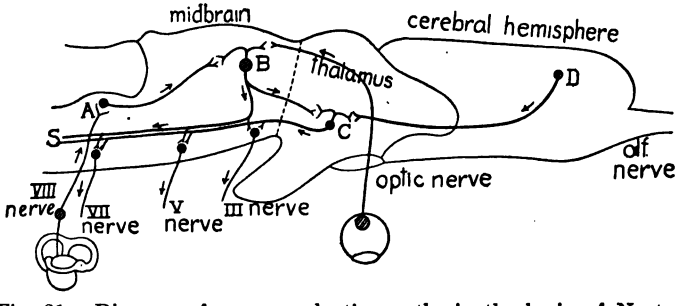

Fig. 21.—Diagram of some conduction paths in the brain of Necturus, seen in longitudinal section. From the medulla oblongata an acoustic impulse may be carried forward through the neuron *A* to the midbrain, whose neurons, *B*, are of the type shown in Fig. 20, receiving both acoustic and optic impulses. This neuron, *B*, may discharge downward through the tract *S* to the motor nuclei of the III, V, VII, etc., nerves, or it may discharge upward to a neuron of the thalamus, *C*, which also receives descending impulses from the cerebral hemisphere through the neuron, *D*, and, in turn, discharges through the motor tract, *S*.

alone, but that they do react to tactual and visual stimuli. When these reactions are carefully measured, it is found that the sound of an electric bell occurring simultaneously with a tactual or visual stimulus markedly increases (reinforces) the strength of the reaction.

The reflex centers of the midbrain are further complicated by the fact that the efferent tract from the sensory centers above the aqueduct of Sylvius is not simple as diagrammed in Fig. 20, but it divides into a descending and an ascending path, as shown by the neuron *B* of Fig. 21. The descending path

connects directly with motor centers, including the oculomotor, bulbar, and spinal motor nuclei (Fig. 21, *S*), while the ascending path enters the thalamus, where associations of a still higher order are effected through the thalamic neuron, *C*. Here again is introduced a physiological choice or dilemma; the response is not a simple mechanical resultant of the interacting stimuli, but its character may be influenced by variable physiological states. The invariable type of action is replaced by a relatively variable or labile type (see p. 32). In the thalamus the nervous impulse is again subjected to modification under the influence of a still greater variety of afferent impulses, for these centers receive all sensory types found in the midbrain, and, in addition, important descending tracts from the cerebral hemispheres (in lower vertebrates the latter are chiefly olfactory).

The more complicated associations are effected by arrangements of correlation tracts and centers illustrated in the simplest possible form by Fig. 18, E. The mode of operation of such a system may be illustrated by an example: A collie dog which I once owned acquired the habit of rounding up my neighbor's sheep at very unseasonable times. The sight of the flock in the pasture (stimulus *R*1, Fig. 18, E) led to the pleasurable reaction (*E*1) of chasing the sheep up to the barnyard. It became necessary to break up the habit at once or lose a valuable dog at the hands of an angry farmer with a shotgun. Accordingly, I walked out to the pasture with the dog. She at once brought in the sheep of her own accord and then ran up to me with every expression of canine pride and self-satisfaction, whereupon I immediately gave her a severe whipping (stimulus *R*2). This called forth the reaction (*E*2) of running home and hiding in her kennel. The next day (the dog and I having meanwhile with mutual forgiveness again arrived at friendly relations) we took a walk in a different direction, in the course of which we unexpectedly met another flock of sheep. At sight of these the dog immediately, with no word from me, put her tail between her legs, ran home as fast as possible, and hid in her kennel. Here the stimulus *R*1 led not to its own accustomed response, *E*1, but to *E*2, evidently under the influence of vestigeal traces of the previous

day's experience, wherein the activities of $C1$ and $C2$ were related through the associational tract (A, A) passing between them.

In the case of the dog's experience just described the neural mechanism was undoubtedly much more complex than our diagram, though similar in principle, and the associative memory process involved was probably vividly conscious (cf. p. 330). But the simpler types of "associative memory" which have been experimentally demonstrated in many of the lower organisms may involve no more complex mechanism than this diagram, and it is by no means certain that any conscious process is there present.

From the preceding account it is clear that isolated individual reflexes are rarely seen in ordinary behavior, but that these are usually compounded so as to mask their specific characteristics. Clinical neurologists find that the reflexes give very valuable signs of the health or disease of particular parts of the nervous system and they have, accordingly, developed special tests for characteristic reflex signs, such as the wink reflex, pupillary reflex, knee jerk, etc.

Since many of the reflexes are normally under continuous control (either conscious or unconscious) by the cerebral cortex, the physiologists have investigated the reflexes of particular parts of the nervous system by separating them in the anesthetized animal from their cortical connections. Thus, if the upper part of the spinal cord is cut across, we have the so-called spinal animal in which spinal reflexes may be studied without the complications arising from the cerebral connections.

The "spinal frog" exhibits no power of spontaneous movement apart from direct peripheral excitation; but pinching the toes will cause a reflex withdrawal of the foot, and many other perfectly coördinated movements may be called forth by appropriate stimulation. The reflexes of the "spinal dog" have been very carefully investigated by Sherrington (see his Integrative Action of the Nervous System) and various coördinated movements characteristic of the locomotor reflexes, scratching, etc., have been thus experimentally studied and the details of their neuromuscular mechanisms determined.

In the frog whose spinal cord has been cut across there is a transient disturbance of the lower spinal reflexes which, however, soon show very perfect coördination. In the spinal dog the reflex disturbance is greater and more enduring, though ultimately very complete reflex coördination is regained. In man after complete transverse section of the spinal cord there is temporary loss of nearly all spinal reflexes; some of these may be regained, though the recovery is never as complete as in the dog (see p. 145).

This interference with spinal reflexes by cutting the connection between the spinal cord and the brain is known as *spinal shock*, and the fact that spinal shock is more severe and more permanent as we pass from lower to higher vertebrates suggests that in the course of evolution the brain (especially the cerebral cortex) has acquired an increasingly greater control over the lower and more primitive reflex centers. There is independent evidence that this is true.

Sherrington (1906, p. 246) believes that spinal shock results from interruption of the pathways descending from centers in the midbrain and medulla oblongata for static and equilibratory adjustments related chiefly with the eye and the labyrinth of the ear. In man there is normally a larger cortical participation in the postural adjustments; accordingly, transverse division of the spinal cord disorganizes the lower reflexes more seriously than in other animals.

By means of numerous experiments on animals and pathological observations on man the locations of the centers of adjustment for many individual reflexes have been determined. Charts illustrating the precise segments of the spinal cord which control the various reflexes of the trunk and limbs have been constructed (*e. g.*, Reid's chart, p. 147. Such charts are published in the larger manuals of neurology and these are of the greatest practical value to the physician and surgeon in enabling them to determine the exact location of an injury which causes disorder of the reflexes, as well as of voluntary movement and conscious sensibility.

It must be kept in mind that in higher vertebrates all parts of the nervous system are bound together by connecting tracts (internuncial pathways). Some of these tracts are long, well-defined bundles of myelinated fibers whose connections are such as to facilitate uniform and clear-cut responses to stimulation. Others are very diffuse and poorly integrated. Permeating the entire central nervous system is an entanglement of very delicate short unmyelinated fibers. This nervous feltwork (neuropil) is much more highly developed in some parts of the brain than in others. It is not well adapted to conduct definite nervous impulses for long distances, but it may serve to diffuse or irradiate such impulses widely. Where tissue of this sort is mingled with myelinated fibers it is termed the "reticular formation" (see pp. 137, 172, 341).

These manifold connections are so elaborate that every part of the nervous system is in nervous connection with every other part, directly or indirectly. This is illustrated by the way in which the digestive functions (which normally are quite autonomous, the nervous control not going beyond the sympathetic system, see p. 270) may be disturbed by mental processes whose primary seat may be in the association centers of the cerebral cortex; and also by the way in which strychnin-poisoning seems to lower the neural resistance everywhere, so that a very slight stimulus may serve to throw the whole body into convulsions.

It follows that the localization of cerebral functions can be

only approximate. Every normal activity has what Sherrington calls its reflex pattern, whose anatomical basis is a definite reflex path; but the stimulus is rarely simple and the nervous discharge irradiates more or less widely, so that the activity is by no means limited to the part which gives the act its reflex pattern. Moreover, neither the stimulus complex nor the character of the irradiation will be repeated exactly in any higher animal, so that the precise nature of the response cannot in any case be infallibly predicted except under experimental conditions (and not always then).

Our picture of the reflex act in a higher animal will, then, include a view of the whole nervous system in a state of neural tension. The stimulus disturbs the equilibrium at a definite point (the receptor), and the wave of nervous discharge thus set up irradiates through the complex lines determined by the neural connections of the receptor. If the stimulus is weak and the reflex path is simple and well insulated, a simple response may follow immediately. Under other conditions the nervous discharge may be inhibited before it reaches any effector, or it may irradiate widely, producing a very complex reflex pattern. In the former case the neural equilibrium will be only locally disturbed; in the latter case almost the whole nervous system may participate in the reaction, a part focal and sharply defined and the rest marginal, diffuse, and exercising more or less of inhibitory or reinforcing control on the final reaction.

The mechanism of the reflex should not be regarded as an open channel through which energy admitted at the receptive end-organ is transmitted to be discharged into the effector organ. It is rather a complex apparatus containing reserves of potential energy which can be released upon the application of an adequate stimulus in accordance with a pattern determined by the inherent structure of the apparatus itself. In other words, the nervous *discharge* is not a mere transmission of the energy of the stimulus, but it implies active consumption of material and release of energy (metabolism) within both the nerve centers and the nerve-fibers. The energy acting upon the effector organ may, therefore, be different in both

kind and amount from that applied to the receptive end-organ. The response likewise involves the liberation of the latent energy of the effector (muscle or gland), the nervous impulse serving merely to release the trigger which discharges this reserve energy.

Further consideration of the nature of the mechanism of the more complex reflexes brings out certain physiological differences between the afferent ("sensory") and the efferent limbs of the arc. To any particular complex of stimuli there is a single most appropriate response. It is the function of the correlation centers to receive the afferent nervous impulses from the sense organs, and as a result of the mutual interaction of these impulses to integrate them and direct the discharge into the particular final common path which will call forth the appropriate response. These correlating mechanisms are sometimes extraordinarily complex and their activities require a very appreciable time. Here, then, is the explanation of the central delay or pause which is characteristic of all reactions involving the correlation centers (see p. 104). This process of correlation and integration of sensory impulses is effected on the afferent side of the reflex arc, and it results in establishing the character of the response to follow before the turning point into the efferent path has been reached.

The efferent side of the arc, on the other hand, has merely to transmit the necessary nervous impulses to the motor neuron systems required for the execution of the movement in the shortest possible time. The so-called motor centers, accordingly, discharge by simple and very direct nervous pathways with the minimum number of synapses between them and the organs of response. This is the neurological basis of the distinction made on p. 36 between correlation and coördination.

The preceding remarks apply to the mechanisms of conscious actions as well as to the reflexes. The cerebral cortex as a whole is developed within the area of sensory correlation tissue above the sulcus limitans (p. 125, cf. also p. 342). The "motor centers" in the precental gyrus of the cortex represent the turning point from the afferent to the efferent segments of the nervous circuits, and from this point to the lower motor centers the pathway is as short and direct as possible with no interruption by synapses. The chief efferent pathway for voluntary motor impulses is the pyramidal tract (pp. 141, 198, 319, and Fig. 64, p. 152).

The studies of Herrick and Coghill have shown that in the development of the nervous system of Amphibia the first reflex circuits to come to maturity are made up of rather complex chains of neurons so arranged as to permit of only one type of response, viz., a total reaction (the swimming movement), from all possible forms of stimulation, and that in successive later stages this generalized type is gradually replaced by a series of special reflexes involving more diversified movements. Parallel with this process the higher correlation centers are

developed for the integration of the several special reflexes into complex action systems. The simple reflex arc, as illustrated in Fig. 1 (p. 26), which is adapted for the execution of a single movement in response to a particular stimulus, is the final stage in this developmental process, whose initial stages are much more complex and diffuse arrangements of neurons adapted for total reactions of a more general sort.

We have just described the mechanisms of certain reflexes. The question at once arises, In what sense do we know the mechanism of a nervous reaction? Certainly not in the sense that we understand all of the factors involved in nervous conduction and correlation. But we do have a practical knowledge of the combinations of neurons necessary to effect certain definite results, much as the practical electrician may be able to wind a dynamo or build a telephone, even though his knowledge of the theory of electricity be very small.

Summary.—The reflex arcs or reflex circuits rather than the neurons of which these circuits are composed are, from the physiological standpoint, the most important units of the nervous system. Reflex acts are to be distinguished, on the one hand, from the simpler non-nervous reactions known as tropisms and taxes, and, on the other hand, from voluntary acts and acquired automatisms. Many instincts are chain reflexes of very complex sorts, the completion of one reaction serving as the stimulus for the next, and so on in series. The simplest true reflex requires a receptor, a center or adjustor, an effector, and the afferent and efferent conductors which put the center into physiological relation with the receptor and the effector respectively. Five types of reflex circuits were distinguished (see Fig. 18) and illustrations of them given. All of the reflex centers are interconnected by systems of fibers, either in the form of definite tracts or else by more diffuse connections in the neuropil. Localization of cerebral function is, therefore, only approximate, with the possibility of all sorts of interconnection of different reflex systems as occasion may require. This is the neurological basis of the greater plasticity of behavior of higher vertebrates as contrasted with invertebrates and lower vertebrates.

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CHAPTER V

THE RECEPTORS AND EFFECTORS

In the further study of the nervous system as the apparatus of adjustment between the activities of the body and those of environing nature, our first task is the analysis of the receptors (that is, the sense organs); for these are the only places through which the forces of the world outside can reach the nervous system in order to excite its activity.

> "The world is so full of a number of things
> I'm sure we should all be as happy as kings."

But in order to attain this fortunate result it is necessary that we should be able to discriminate the essential from the unimportant elements of this environing complex, and to adjust our own behavior in relation thereto.

Protoplasm in its simplest form is sensitive to some sorts of mechanical and chemical stimulation. In fact, as we have seen, all of the so-called nervous functions are implicit in undifferentiated protoplasm. But the bodies of all but a few of the lowest organisms are protected by some sort of a shell or cuticle from excessive stimulation from the outside, and individual parts of the surface are then differentiated in such a way as to be sensitive to only one group of excitations while remaining insensitive to all other forms. Thus arose the sense organs, each of which consists essentially of specialized protoplasm which is highly sensitive to some particular form of energy manifestation, but relatively insensitive to other forms of stimulation. Each sense organ possesses, in addition, certain accessory parts, adapted to concentrate the stimuli upon the essential sensitive protoplasm, to intensify the force of the stimulus, or to so transform the energy of the stimulus as to enable it to act more efficiently upon the essential end-organ.

Sherrington states the distinctive characteristic of the sense

organs in this form, "The main function of the receptor is, therefore, to *lower the threshold of excitability of the arc for one kind of stimulus and to heighten it for all others.*" The selective function of the receptors is illustrated by a consideration of the different forms of vibratory energy which pervade the environment in which we live.

There are, first, rhythmically repeated mechanical impacts perceived through the sense of touch. This series of tactile sensations extends from a single isolated contact at one extreme to rhythmically repeated contacts touching the skin as frequently as 1552 vibrations per second.

A second series of vibratory phenomena is presented by the mechanical vibrations of the surrounding medium perceived subjectively as sound. Out of the entire series of such vibrations of all possible frequencies the human ear is sensitive to a series of approximately ten octaves from about 30 (in some cases 12) to about 30,000 (in some cases 50,000) vibrations per second (wave lengths from 1228 cm. or 40 ft. to 1.3 cm. or .5 inch in length). To all other vibrations it is insensitive. Within this range the average human ear can discriminate some 11,000 different pitch qualities (Titchener).

Subjectively, the series of tone sensations is broken up into a number of octaves, and it is found that a given tone of the musical scale is excited by vibrations of exactly twice the frequency which excites the corresponding tone of the next lower octave. By analogy with this arrangement all series of physical vibrations are sometimes spoken of as divisible into octaves, the octave being defined as those vibration frequencies which lie between a given rate and twice that rate or half that rate.

A third type of vibratory phenomena is presented by the much more rapid series of so-called ethereal vibrations, or waves in immaterial media. The lower members of this series are the Hertzian electric waves; the higher members are the *x*-rays. Between these extremes lie waves perceived as radiant heat, the light waves, and the ultra-violet rays of the spectrum. This series of ethereal vibrations may extend farther indefinitely both downward and upward, but of its ultimate limits we have no knowledge.

There is no human sense organ which can respond directly to the electric waves, the ultra-violet rays, and the *x*-rays. These have, accordingly, remained wholly unknown to us until revealed indirectly by the researches of the physical laboratories. Some ten octaves of this series are contained in the solar spectrum, from an infra-red wave length of about .1 mm. to an ultra-violet wave length of .00035 mm. The light from metallic arcs and from incandescent gases has, however, been found to contain wave lengths as short as .00006 mm. The human eye is sensitive to something over one octave of this series (waves from .0008 to .0004 mm. in length, whose rates lie between 400,000 and 800,000 billions of vibrations per second), with six octaves in the infra-red and three in the ultra-violet. The lower members of this series of vibrations of the solar spectrum, and to a less extent the higher also, are capable of stimulating the temperature organs of the skin.

Thus it appears that of the complete series of ethereal vibrations, we can sense directly only about one octave by the eye and a number of others through the sense organs for temperature in the skin, while to the lowest and highest members of the series our sense organs are entirely insensitive. The sensitivity of the skin to these vibrations is limited subjectively to a small range of temperature sensations, while the retinal excitations give us subjectively an extensive series of sensations of color and brightness. The human eye can discriminate from 150 to 230 pure spectral tints, besides various degrees of intensity and purity of tone, making a total of between 500,000 and 600,000 possible discriminations by the visual organs (von Kries). Some of the preceding data are summarized in the table[1] on page 77.

Similarly, the chemical senses, taste and smell, reveal to us only a very small number out of the total series of actual excita-

[1] In the preparation of this table I have been assisted by Professor R. A. Millikan, of the University of Chicago, whose kindness I gratefully acknowledge. The figures given are based upon the formula—

$$\frac{\text{velocity}}{\text{wave length}} = \text{rate}$$

and the velocity of transmission is taken as 3×10^{10} cm. per second. The actual velocity of light waves as worked out experimentally by Michelson is 299,853 kilometers per second.

TABLE OF PHYSICAL VIBRATIONS

Physical process.	Wave length.	Number of vibrations per second.	Receptor.	Sensation.
Mechanical contact.	.....	From very slow to 1552 per second.	Skin.	Touch and pressure.
Waves in material media.	Below 12,280 mm.	Below 30 per second.	None.	None.
	12,280 mm. to 13 mm.	30 per second to 30,000 per second.	Internal ear.	Tone.
	Above 13 mm.	Above 30,000 per second.	None.	None.
Ether waves.	∞ to .1 mm. (electric waves).	0 to 3000 billion (3×10^{12}).	None.	None.
	.1 mm. to .0004 mm.	3000 billion (3×10^{12}) to 800,000 billion (8×10^{14}).	Skin.	Radiant heat.
	.0008 mm. to .0004 mm.	400,000 billion (4×10^{14}) to 800,000 billion (8×10^{14}).	Retina.	Light and color.
	.0004 mm. to .000059 mm. (ultra-violet-rays).	800,000 billion (8×10^{14}) to 5,100,000 billion (5.1×10^{15}).	None.	None.
	.0000008 mm. to .00000005 mm. (x-rays).	400,000,000 billion (4×10^{17}) to 6,000,000,000 billion (6×10^{18}).	None.	None.

tions to which our sense organs are exposed. Our organs of taste, in fact, can respond to only four types of chemical substances, with only four subjective sense qualities, viz., sour, salty, sweet, bitter. The organs of smell respond to a larger range of chemical stimuli and to far greater dilutions, *i. e.*, the threshold of sensation is far lower for smell than for taste.

Many of the lower animals have very different limits of susceptibility to the kinds of stimulation which we have just been considering, and in some cases they have sense organs which are attuned to respond to a quite different series of environmental factors than are our own, as, for example, the lateral line sense organs of fishes. We can form no idea how the world appears to such organisms except in so far as their sensory equipment is analogous with our own.

From these illustrations it is plain that the sensory equipment of the human body is adapted to respond directly to only

a limited part of the environing energy complex, the remainder having little, if any, practical significance in the natural environment of primitive man. During the progress of the development of human culture mankind has very considerably widened his contact with the environment by artificial aids to his sense organs. The range of vision has been extended by the microscope and the telescope, and of hearing by the microphone and the telephone. The photographic plate enables him to extend his knowledge of the solar spectrum beyond its visible limits, and the Marconi wireless apparatus brings the Hertzian electric waves under his control and thus enables him to put a girdle round about the earth in less than Puck's forty minutes.

We may conceive the body as immersed in a world full of energy manifestations of diverse sorts, but more or less completely insulated from the play of these cosmic forces by an impervious cuticle. The bodily surface, however, is permeable in some places to these environing forces and in a differential fashion, one part responding to a particular series of vibrations, another part to a different series, much as the strings of a piano when the dampers are lifted will vibrate sympathetically each to its own tone when a musical production is played on a neighboring instrument. The sense organs, again, may be compared with windows, each of which opens out into a particular field so as to admit its own special series of environmental forces. In each species of animals these windows are arranged in a characteristic way, so as to admit only those forms of energy which are of practical significance to that animal as it lives in its own natural environment.

The sensory equipment of the human race was thus established by the biological necessities of our immediate animal ancestors, and there is no evidence of subsequent improvement in these peripheral physiological mechanisms or of any increase in the number of our senses during the advancement of human culture. The advance in efficiency of the human race as compared with its brutish ancestors is to be sought rather in a more efficient central apparatus in the brain for the utilization of the sensory data for the welfare of the organism. What the progress of science has accomplished is to supplement the limited

sensory equipment of primitive man by various indirect means. To recur to our analogy of a house with many windows, we have not been able to increase the number of windows so as to look out directly into new fields; but we have increased the range of vision through the old windows, much as a telescope brings remote objects near and as a periscope enables the observer to see around a corner. To the development of the cerebral cortex we owe the acquisition of these new powers which have opened to us the realms of electric vibrations, ultra-violet rays, and many other natural phenomena to which our unaided sense organs are quite insensitive.

Children in the kindergarten are taught that there are five senses. In reality, there are more than twenty different senses. Some of the sense organs are stimulated by external objects and hence are termed *exteroceptors;* others are stimulated by internal excitations of the visceral organs and are termed *interoceptors.* Still further classifications have been suggested, to which reference will be made shortly. Here we must first consider the criteria in accordance with which the various senses are distinguished.

The analysis and classification of the senses is by no means so simple a task as one might at first suppose. It is true that ordinarily we do not confuse a thing seen with a sound heard; but, on the other hand, we do constantly confuse savors with odors, and it often requires refined physiological experimentation to determine whether the organ of taste or the organ of smell is the source of the sensory excitation in question. Most of the common "flavors" of food are, in reality, odors and are perceived by the organ of smell only. A bad cold which closes the posterior nasal passages makes "all food taste alike" for this reason. In reality, as we have already seen, there are only four tastes recognized by the physiologists, viz., sweet, sour, salty, and bitter.

Confusion has arisen in the attempts to analyze these two senses from the fact that different physiologists have used different definitions of a "sense." One author, who defines these senses in terms of the physical agents which excite them, says that taste is stimulated by liquids and smell by vapors, and that, accordingly, aquatic animals, whose nostrils are filled

with water, have by definition no sense of smell. Other authors separate these senses according to the organ stimulated, the excitation of the nose being smell, that of the taste-buds being taste, regardless of the nature of the exciting substance or of the subjective quality of the sensation.

There are, in reality, four different factors which must be taken into account in defining a "sense." (1) Doubtless with us human folk the most important criterion is direct introspective experience, the *psychological criterion.* Ordinarily this is adequate, but, as we have just seen, there are some cases where it alone cannot be depended upon to distinguish between two senses. (2) The adequate stimuli of the various senses exhibit characteristic physical or chemical differences, the *physical criterion.* This factor, too, must be carefully investigated or we may be led astray. (3) The data of anatomy and experimental physiology may differentiate structurally the receptive organs and conduction paths of the several types of sensation, the *anatomical criterion.* (4) Finally, the type of response varies in a characteristic way for the different senses, the *physiological criterion.*

The fourth criterion has been applied to solve the problem of the reason for the development of two very different types of sense organs and cerebral connections for the senses of smell and taste, both of which are chemical senses with similar subjective qualities. It has been pointed out by Sherrington that taste is an interoceptive sense, calling forth visceral responses within the body, while smell is, in part at least, an exteroceptive sense, being excited by objects at a distance from the body and calling forth movements of locomotion carrying the whole body toward or away from the source of the odorous emanations. Thus the form of the response is here the distinctive factor, and incidental to this feature the organs of smell are sensitive to far smaller quantities of the stimulating substance than are the taste-buds. Parker and Stabler have shown that the human organ of smell is sensitive to alcohol at a dilution 24,000 times greater than that necessary to stimulate the organs of taste (see p. 244).

It is impossible in the present state of our knowledge to frame adequate definitions of all the senses in terms of any

one of these four criteria alone, although it is a reasonable hope that this may at some future time be attained. Even when all of these criteria are taken into account, it is by no means easy to determine how many separate senses the normal human being possesses. Not only is there a considerable number of sense organs not represented at all in our traditional list of five senses, but several of these five are complex. Thus, the internal ear includes two quite distinct organs—the cochlea, which serves as a receptor for sounds, and the labyrinth, whose semicircular canals serve as the chief sense organs concerned in the regulation of bodily position and the maintenance of equilibrium, functions which are quite distinct from hearing. The skin, too, serves not only as the chief organ of touch, but also the additional functions of response to warm, cold, and painful impressions, besides some other more obscure sensory activities, such as tickle.

An acceptable classification of the sense organs or receptors of the body must take account of their anatomical relations, of the nature of the physical or chemical forces which serve as the adequate stimuli, of the subjective qualities which we experience upon their excitation, and of the character of the physiological responses which commonly follow their stimulation. The last point has been too much neglected.

In fact, the most fundamental division of the nervous system which we have, cutting down through the entire bodily organization, is based upon this physiological criterion. From this standpoint we divide the nervous organs into two great groups: (1) a somatic group pertaining to the body in general and its relations with the outer environment, and (2) a visceral, splanchnic, or interoceptive group. The latter group comprises the nerves and nerve-centers concerned chiefly with digestion, respiration, circulation, excretion, and reproduction. These are intimately related with the sympathetic nervous system and those parts of the central nervous system directly connected therewith, though the more highly specialized members of this group are independent of the sympathetic system. The somatic group comprises the greater part of the brain and spinal cord and the cranial and spinal nerves, or, briefly, the cerebro-spinal nervous system as distinguished

from the sympathetic system (see p. 251). This is the mechanism by which the body is able to adjust its own activities directly in relation to those of the outside world—to procure food, avoid enemies, and engage in the pursuit of happiness.

The organs belonging to each of these two groups do much of their work independently of the other group, *i. e.*, visceral stimuli call forth visceral responses and external or somatic stimuli call forth somatic responses. Nevertheless, the two groups of organs are by no means entirely independent, for external excitations may produce strong visceral reactions, and conversely. Thus, the sight of luscious fruit (exteroceptive stimulus) naturally calls forth movements of the body (somatic responses) to go to the desired object and seize it. But if one is hungry, the mouth may water in anticipation, a purely visceral response. On the other hand, the strictly visceral (interoceptive) sensation of hunger is apt to set in motion the exteroceptive reactions necessary to find a dinner.

Sherrington, whose analysis with some modifications is here adopted, recognizes three types of sense organs or receptors: (1) the *interoceptors*, or visceral receptive organs, which respond only to stimulation arising within the body, chiefly in connection with the processes of nutrition, excretion, etc.; (2) the *exteroceptors*, or somatic sense organs, which respond to stimulation arising from objects outside the body; (3) the *proprioceptors*, a system of sense organs found in the muscles, tendons, joints, etc., to regulate the movements called forth by the stimulation of the exteroceptors. This third group is largely subsidiary to the somatic group, or exteroceptors, and will be considered more in detail below.

The proprioceptive sense organs are deeply embedded in the tissues and are typically excited by those activities of the body itself which arise in response to external stimulation. The proprioceptors then excite to reaction the same organs of response as the exteroceptors and regulate their action by reinforcement or by compensation or by the maintenance of muscular tone. All reactions concerned with motor coördination, with maintenance of posture or attitude of the body, and with equilibrium involve the proprioceptive system.

The distinction between somatic and visceral systems of organs and

nerves is variously drawn by different neurologists depending upon whether anatomical, embryological or physiological criteria are given greater weight. According to the usage here adopted, somatic organs and nerves are, in general, concerned with responses to external stimulation in which the body or its members are oriented with reference to these stimuli, the response being excited through the exteroceptors and the course of the reaction controlled through the proprioceptors. Visceral organs and nerves, on the other hand, are concerned with responses to internal stimulation through the interoceptors which involve no spatial orientation of the body.

The nerves of proprioceptive sensibility were first experimentally demonstrated and their significance clearly explained by Sir Charles Bell more than a century ago (see the references cited on p. 158).

The important point to bear in mind here is that stimulation of the visceral sense organs typically calls forth visceral responses, *i. e.*, adjustments wholly within the body, while stimulation of the somatic sense organs typically calls forth somatic responses, *i. e.*, a readjustment of the body as a whole with reference to its environment. This is a very fundamental distinction. These two functions are quite diverse and the organization of these two parts of the nervous system shows corresponding structural differences.

The internal adjustments of the visceral systems are effected by a nicely balanced mechanism of local and general reflexes so arranged that most of their work is done quite mechanically and unconsciously. The taking of food and its preliminary mastication are generally voluntary acts whose various processes are—or may be—controlled at will. But once the food has passed into the esophagus, the further work of swallowing, digestion, and assimilation is no longer under direct control. The presence of a morsel of food in the upper part of the esophagus excites the muscular movements necessary for the completion of the act of swallowing, which no act of will can prevent or modify. In fact, any attempt at conscious interference or regulation is apt to result in an incoördination of the movements involved, and sputtering or gagging may result.

The mechanisms involved in these processes are inborn and require no practice for their perfect performance. They are innate, invariable, and essentially similar in all members of a race or species. They are, moreover, nicely adapted to the mode of life characteristic of the species. In a carnivorous

animal the whole physiological machinery of nutrition is different from that of a herbivorous animal. These physiological and structural peculiarities by which each species of animal is adapted to its mode of life have been brought about by natural selection and other evolutionary factors. This is not absolutely true of all visceral actions; some are acquired and modifiable. But as a general rule this is their type.

Some of the somatic actions are likewise innate and relatively fixed in character. This is true of most of the proprioceptive reactions and of many of the exteroceptive as well. Fish can swim as soon as they are hatched; chicks just out of the shell have an instinctive tendency to peck at all small objects on the ground. But in most of these cases (of which innumerable instances might be cited) some practice is necessary before perfect responses are attained; and a very large proportion of the exteroceptive acts are not innate, but acquired by long and often arduous experience. In higher vertebrates, as a rule, all but the simplest and most elementary exteroceptive activities are individually acquired, variable, non-hereditary, plastic behavior types. The elements of which these acts are made up are, of course, necessarily present in the inherited reflex pattern; but the pattern according to which these elements are combined is not wholly predetermined in the hereditary organization of the species (pp. 32, 338).

With these principles in mind, let us now undertake an analysis of the human receptors and of the nervous end-organs related to their effectors, or organs of response. The following list is by no means complete and is in some parts merely provisional.

I. SOMATIC RECEPTORS

These are concerned with the adjustment of the body to external or environmental relations.

A. The Exteroceptive Group

The sense organs of this group are stimulated by objects outside the body and typically call forth reactions of the whole body, such as locomotion, or of its parts, so as to change the relation of the body to its environment. This group includes a system of general cutaneous sense organs, some organs of deep sensibility, and some of the higher sense organs. The cutaneous exteroceptors comprise a very complex system whose

analysis has proved very difficult. The correlation of the data of physiological experiment with the anatomical structure of the cutaneous end-organs is still somewhat problematical and the assignment of end-organs here to the various cutaneous senses should be regarded as provisional rather than as demonstrated.

1. **Organs of Touch and Pressure.**—These fall into two groups, those for deep sensibility (pressure) and those for cutaneous sensibility (touch).

The *deep pressure sense* is served by nerve-endings throughout the tissues of the body and is preserved intact after the loss of all cutaneous nerves. Most of the functions of the deep sensory nerves belong to the

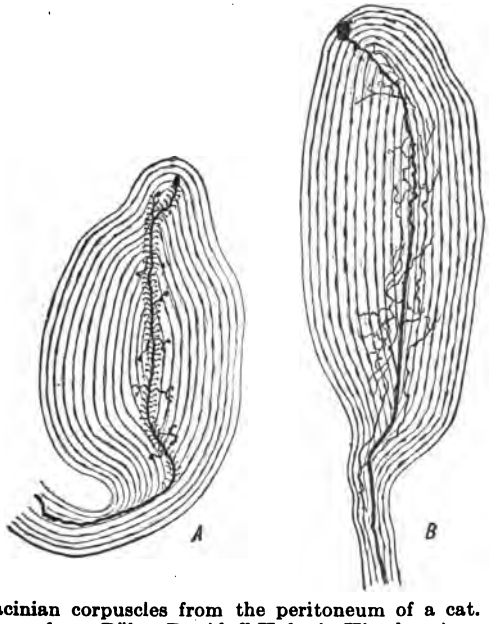

Fig. 22.—Pacinian corpuscles from the peritoneum of a cat. (After Sala, from Böhm-Davidoff-Huber's Histology.)

proprioceptive and interoceptive series (see below), but some exteroceptive functions are here present also. The latter are probably related chiefly to the Pacinian corpuscles and similar encapsulated end-organs. The Pacinian corpuscle has a central nerve-fiber enclosed in a firm lamellated connective-tissue sheath (Fig. 22). By these end-organs relatively coarse pressure may be discriminated and localized (exteroceptive function), and movements of muscles and joints can be recognized (proprioceptive function). The sensory fibers concerned with the deep pressure-sense are distributed through the muscular branches of the spinal nerves in company with the motor fibers. The point stimulated can be localized with a fair degree of accuracy.

The *cutaneous organs of tactile sensibility* are of several kinds, whose precise functions are still obscure. There are two principal groups of these, those arranged in the hair bulbs at the roots of the hairs and those on the hairless parts, such as the lips, the palms of the hands, and the soles of the feet. The latter are more highly differentiated endings and are organs of the most refined active touch.

Most of the surface of the body is more or less hairy, though many of these hairs may be so fine as to escape observation. The hairs are the

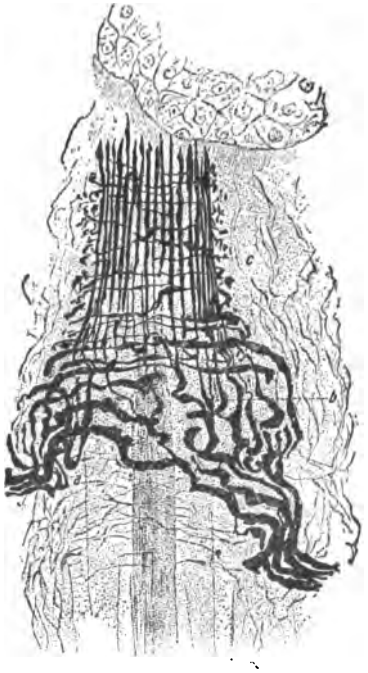

Fig. 23.—Nerve-endings about a large hair from the dog. The nerve-fibers are shown in black surrounding the hair shaft, the straight fibers at *b* and the circular fibers at *c*. (After Bonnet, from Barker's Nervous System.)

most important sources of excitation of the first group of cutaneous sense organs, and the sensitiveness of the hair-clad parts is greatly reduced after the hair is shaved. The threshold of excitation to touch of the skin about the base of a hair is from three to twelve times higher than that of a similar excitation applied to the hair itself. The innervation of the hair bulbs is very complex and varies greatly for different animals and for the different kinds of hairs on the same body, so that no general description is possible.

Miss Vincent has shown that the large vibrissæ of the rat receive their nerve-supply from two sources. A large nerve bundle pierces the deep layer of the skin (dermis) in the lower part of the hair bulb, spreads out over the inner hair follicle in a heavy plexus, and terminates chiefly in a mantle of touch cells, resembling Merkel's corpuscles (see Fig. 26), in the outer root sheath all over the follicle. A second nerve supply comes from the dermal plexus of the skin, from which branches run down and form a nerve ring about the neck of the follicle. Experimental studies show that

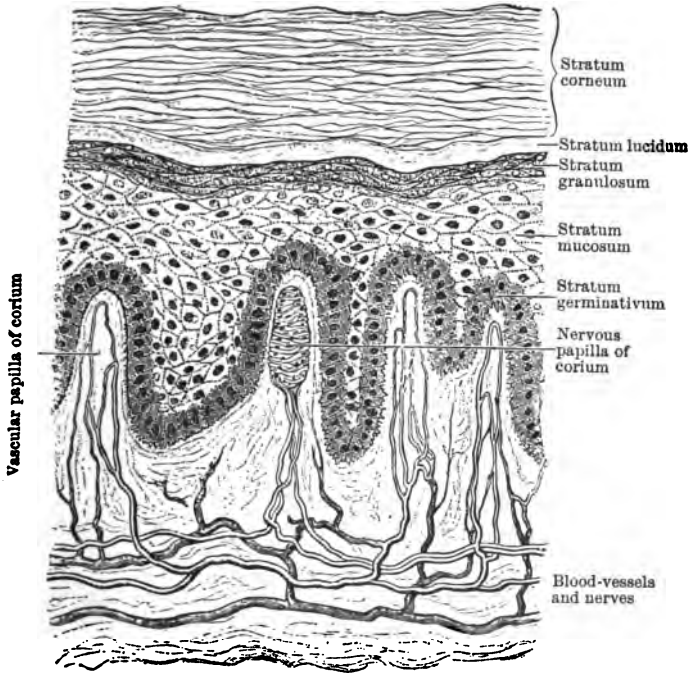

Fig. 24.—Section through the human skin, illustrating the five layers of the epidermis and the papillæ of the dermis or corium. A corpuscle of Meissner is seen within one of the dermal papillæ. (From Cunningham's Anatomy.)

these hairs are very important not only as general tactile organs, but specifically as aids in locomotion and equilibration. The ordinary hairs of man and other mammals have three forms of specific nerve-endings in addition to various forms of terminal arborizations in the surrounding tissues: (1) straight and often forked endings running parallel with the base of the hair; (2) circular fibers forming a plexiform ring around the root of the hair external to the straight endings; and (3) leaf-like nerve-

endings associated with special cells resembling Merkel's corpuscles. Figure 23 illustrates the first and second types of these endings.

Under the hairless parts of the skin there are special tactile bodies, such as Meissner's corpuscles. These are generally found in the deep layer of the skin (dermis) and in the underlying tissues, either as free skein-like terminal aborizations of cutaneous nerves or as similar more elaborate endings enclosed in connective-tissue capsules. Figures 24 and 25 illustrate the most highly differentiated form of these endings, the Meissner corpuscles. Merkel's corpuscles (Fig. 26), which are found in the epidermis and elsewhere, are probably simpler organs of this system.

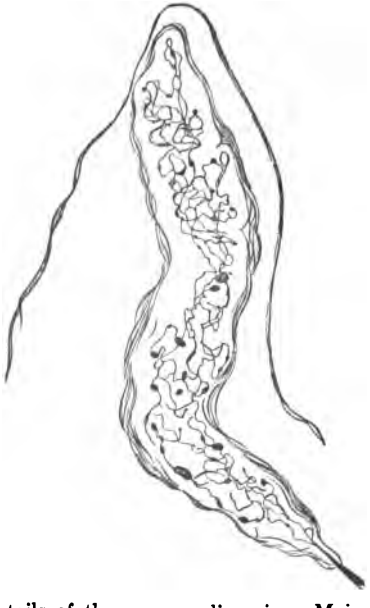

Fig. 25.—The details of the nerve-endings in a Meissner corpuscle from the human skin. Only the outline of the corpuscle is shown, within which the terminals of the nerve-fiber form a complex skein. (After Dogiel, from Böhm-Davidoff-Huber's Histology.)

All forms of cutaneous sensibility (touch, temperature, and pain) when studied physiologically are found to be localized in small areas or sensory spots, each of which has a specific sensibility to one only of the cutaneous sensory qualities. The intervening parts of the skin are insensitive. An immense amount of physiological and clinical observation has been devoted to the analysis of cutaneous sensibility, including the experimental division of cutaneous nerves in their own bodies by Head, Trotter and Davies, and Boring for the purpose of studying more critically the distribution of the various sensory functions in and round the anesthetic

areas produced by the injuries and the phenomena accompanying the restoration of these functions during the regeneration of the nerves. But general agreement has not yet been reached on all questions.

Head and his colleagues are of the opinion that all forms of cutaneous sensibility (touch, temperature, and pain) are grouped in two series, each

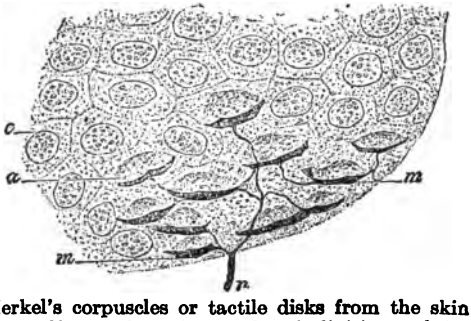

Fig. 26.—Merkel's corpuscles or tactile disks from the skin of the pig's snout. The nerve-fiber, *n*, branches, and each division ends in an expanded disk, *m*, which is attached to a modified cell of the epidermis, *a*. The unmodified cells of the epidermis are shown at *c*. (From Ranvier.)

served by different nerve-fibers and end-organs; these he terms "protopathic" and "epicritic" sensibility. *Protopathic sensibility* is subjectively general diffuse sensibility of a primitive form. Its sense organs are arranged in definite spots, and yet these sensations have no clear local reference or sign; that is, the spot stimulated cannot be accurately localized. There are separate spots for touch, heat, cold, and pain; these

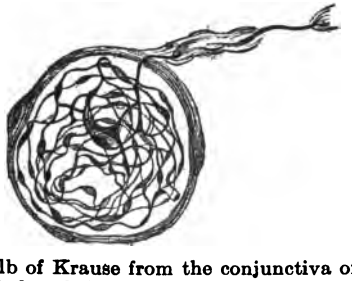

Fig. 27.—End-bulb of Krause from the conjunctiva of man. The nerve-ending forms a globular skein within a delicate connective-tissue capsule. (After Dogiel.)

spots being generally grouped near the hair bulbs. In fact, the hairs are the most important tactile organs of this system and the other sense qualities belonging here are intimately associated with the roots of the hairs. *Epicritic sensibility* is a more refined sort of discrimination and is regarded as a later evolutionary type. It includes light touch, on the

hairless parts of the body particularly, and the discrimination of the intermediate degrees of temperature. Cutaneous localization and the discrimination of the distance between two points simultaneously stimulated (the "compass test") are functions of this system; but pain sensibility is not included, this being wholly protopathic.

Trotter and Davies repeated some of Head's experiments and, while confirming most of his observations, they were led to somewhat different conclusions. They do not regard the protopathic and epicritic series as served by distinct systems of nerves, but as different physiological phases of the same systems of nerve-fibers and end-organs. Carr subjected Head's own data to critical analysis and concluded that these data do not support the distinction between the protopathic and epicritic types of sensibility. Boring repeated Head's experimental division of a cutaneous nerve in his own body and substituted for Head's conception of separate protopathic and epicritic systems of nerves a theory of dual innervation of sensory spots. Head has replied to these critics in the appendix to his collected papers (1920). Still more recently Pollock (1919, 1920), after study of over 1000 military cases suffering from injuries of peripheral nerves, concluded that in regenerating nerves the return of so-called protopathic sensibility earlier than that of epicritic sensibility is due to the overlap of the field of distribution of adjacent nerves and is not a sign of earlier regeneration of protopathic fibers, as Head supposed. In other words, there is no temporal dissociation of protopathic and epicritic sensibilities. This appears to support the hypothesis of dual innervation proposed by Boring

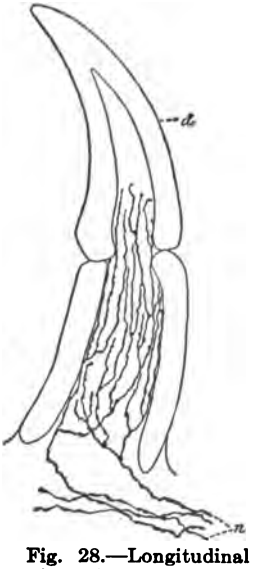

Fig. 28.—Longitudinal section of a tooth of a fish, Gobius, showing nerve terminals: *d*, dentin; *n*, nerve-fibers entering the cavity of the dentin and ending free. (After Retzius, from Barker's Nervous System.)

2. **End-organs for Sensibility to Cold.**

3. **End-organs for Sensibility to Heat.**—Physiological experiment shows that warmth and cold are sensed by different parts of the skin (the warm spots and the cold spots respectively), and Head is of the opinion that each of these types of sensibility may be present in an epicritic and a protopathic form. What end-organs are involved here is by no means certain. The margin of the cornea was found by von Frey to be sensitive to pain and cold only. The free nerve-endings found here he assumes to be pain receptors and the end-bulbs of Krause (Fig. 27) to be cold receptors. By an analogous argument he assumes that the "genital corpuscles" of Dogiel and some similar endings widely distributed in the skin are warmth receptors. By some other physiologists these types of corpuscles are regarded as belonging to the tactile system. Stimulation of the somatic nerves of deep sensibility causes no temperature sensations. (For temperature sensations in the viscera see p. 271.)

4. End-organs for Pain.—Some physiologists believe that there are separate nerve-endings for pain; others regard pain as a quality which may be present in any sense, and not as itself a true sensation (pp. 279ff.). The free nerve-endings among the cells of the epidermis are regarded by von Frey as the pain receptors, because these endings alone are present in some parts of the body where susceptibility to pain is the only sense quality present, such as the dentin and pulp of the teeth (Fig. 28), the cornea, and the tympanic membrane of the ear (J. G. Wilson).

Similar endings are found throughout the epidermis (Fig. 29) and in many deep structures. The nerves of deep sensibility of the somatic sensory type may also carry painful impressions. (For visceral pain see pp. 272, 280.) According to Head, cutaneous pain is wholly of protopathic type, and in case of injury to the peripheral nerves it disappears and reappears in regeneration simultaneously with the protopathic type of tactile and temperature sensation. This cutaneous pain is not accurately localizable unless epicritic cutaneous sensibility is also present. On the possible relation of sympathetic nerves to pain see page 197.

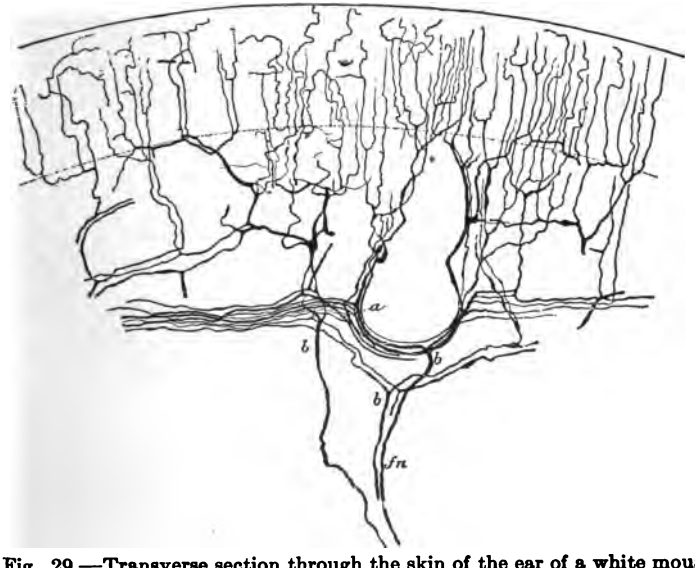

Fig. 29.—Transverse section through the skin of the ear of a white mouse. The dotted line marks the lower border of the epidermis: *a*, horizontal nerve-fibers; *b*, bifurcation of nerve-fibers; *fn*, cutaneous nerve-fibers. (After Van Gehuchten, from Barker's Nervous System.)

5. End-organs of General Chemical Sensibility.—In man this type of sensibility is found only on moist epithelial surfaces, such as the mouth cavity; but in fishes it may be present over the entire surface of the body. The sense organ is probably the free nerve terminals among the cells of the epithelium, never special sense organs like taste-buds, for these when present in the skin belong to a quite different system.

6. **Organs of Hearing.**—The stimulus is material vibrations whose frequency ranges from 30 to 30,000 per second (see p. 75). The receptor is the spiral organ (organ of Corti) in the cochlea of the ear (see p. 221), and perhaps also the sensory spots in the saccule and utricle. There are two forms of auditory sensations: (1) noise, stimulated by sound concussions or irregular mixtures of aërial vibrations; (2) tone, stimulated by sound waves or periodic aërial vibrations.

7. **Organs of Vision.**—The stimulus is ethereal vibrations ranging between 400,000 billions and 800,000 billions per second. Here also there are two forms: (1) brightness, stimulated by mixed ethereal vibrations; (2) color, stimulated by simpler ethereal vibrations. (On the structure of the eye and its connections see p. 230.)

8. **Organs of Smell.**—This sense has both exteroceptive and interoceptive qualities, the latter being apparently the more primitive. (See pp. 80, 97, and 241.)

B. The Proprioceptive Group

These sense organs are contained within the skeletal muscles, joints, etc., and are stimulated by the normal functioning of these organs, thus reporting back to the central nervous system the exact state of contraction of the muscle, flexion of the joint, and tension of the tendon. Cutaneous sensibility may also participate in these reactions, which are generally unconsciously performed.

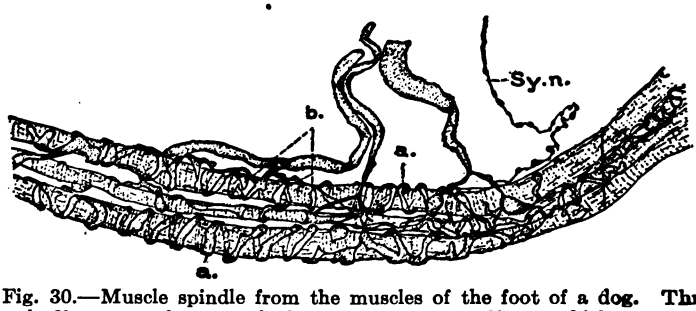

Fig. 30.—Muscle spindle from the muscles of the foot of a dog. Three muscle-fibers are shown and three sensory nerve-fibers, which enter the muscle spindle, branch, and wind spirally around the muscle-fibers (*a*, *b*). A sympathetic nerve-fiber (*Sy.n.*) also enters the muscle spindle. (After Huber and DeWitt, from Barker's Nervous System.)

9. **End-organs of Muscular Sensibility.**—The organ is a series of nerve-endings among special groups of muscle-fibers known as muscle spindles. These endings are usually spirally wound around their muscle-fibers and are stimulated by the contraction of the muscle (Fig. 30).

As we shall see below (p. 98), the muscles are classified for our purposes into three groups: (1) somatic muscles (the striated skeletal muscles); (2) general visceral muscles (generally unstriated and involuntary); and (3) special visceral muscles of the head which are striated and voluntary. The first and third of these groups receive their motor innervation from

cerebrospinal nerves; the second, from sympathetic nerves. The classification of the nerves of muscle sense related respectively to these three groups of muscle offers some difficulties. Those related with the first group are the typical proprioceptors; those of the second group are clearly interoceptors. The striated muscles of the third group often act in response to exteroceptive stimuli or voluntarily; yet, since these muscles are here classed as a special visceral group, their organs of muscle sense should logically be regarded as highly specialized interoceptors, though any such rigid classification is, in fact, arbitrary and fails to recognize the ambiguous position of these special muscles.

10. End-organs of Tendon Sensibility.—Nerve-endings are spread out over the surface of tendons and are stimulated by stretching the tendon during muscular contraction (Fig. 31).

11. End-organs of Joint Sensibility.—Nerve-endings found in the joints and the surrounding tissues are stimulated by bending the joint,

Fig. 31.—A teased preparation of a tendon of a small muscle from a rabbit, showing the endings of the nerve-fibers of tendon sensibility, each of which spreads out widely over the surface of the tendon. (After Huber and DeWitt, from the Journal of Comparative Neurology.)

and report back to the central nervous system the degree of flexion of the joint. The chief end-organs are probably Pacinian corpuscles (see Fig. 22).

12. Organs of static and equilibratory sensation arising from stimulation of the semicircular canals of the internal ear (Fig. 32). This is the most highly specialized member of the proprioceptive group and acts in conjunction with all of the other somatic senses to maintain equilibrium, posture, and the tone of the muscular system (see p. 202). The eyes and most of the other exteroceptive sense organs, so far as they act in the way just suggested, also serve as proprioceptors.

II. VISCERAL RECEPTORS

The visceral or interoceptive senses fall into two well-defined groups: First, the general visceral systems are without highly specialized end-organs and are innervated through the sympathetic nervous system. Their reactions are chiefly unconsciously performed. Second, the special visceral senses are provided with highly developed end-organs which are innervated directly from the brain without any connection with the sympathetic nervous system. The special visceral sense organs may in some cases serve as exteroceptors as well as interoceptors. Their reactions may be conscious and voluntary.

A. General Visceral Group

Many of the sensations of this group are obscure and a number of excito-motor and excito-glandular reactions may be included here which

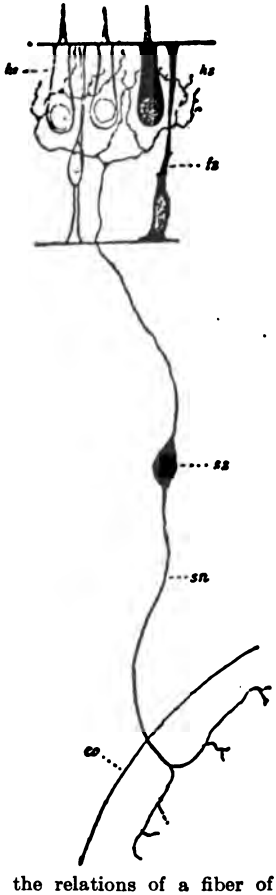

Fig. 32.—Diagram of the relations of a fiber of the vestibular branch of the auditory nerve and its mode of termination in the semicircular canal: *co*, the central nervous system; *fz*, non-nervous supporting cell of the semicircular canal; *hz*, hair cell, one of the receptor cells of the sensory surface; *sn*, axon of the vestibular neuron; *sz*, cell body of the vestibular neuron. (After Retzius, from Barker's Nervous System.)

never come into clear consciousness, particularly those concerned with nutrition, excretion, and vasomotor adjustments. The number of these

reactions might be considerably increased; for further discussion of these reflexes see p. 263.

13. **Organs of Hunger.**—The stimulus is strong periodic contractions of the muscles of the stomach. Hunger is apparently a variety of muscle sense, but other factors are also present (see p. 270).

14. **Organs of Thirst.**—The specific stimulus here is probably a drying of the pharyngeal mucous membrane, together with more general conditions.

15. **Organs of Nausea.**—The stimulus is probably an antiperistaltic reflex in the digestive tract (see p. 272).

16. **Organs giving rise to respiratory sensations,** suffocation, etc. (see p. 265).

17. **Organs giving rise to circulatory sensations,** flushing, heart panics, etc. (see p. 263).

Fig. 33.—Free nerve-endings in the mucous membrane of the esophagus of a cat. (After DeWitt, from Wood's Reference Handbook of the Medical Sciences.)

18. **Organs giving rise to sexual sensations.**

19. **Organs of sensations of distention of cavities,** stomach, rectum, bladder, etc. This is a variety of muscle sense.

20. **Organs of visceral pain** (see pp. 272, 280).

21. **Organs of obscure abdominal sensations** associated with strong emotions of fright, anger, affection, etc., characterized (probably correctly) by the ancients by such expressions as "yearning of the bowels," etc. The stimulus is probably a tonic contraction of the unstriped visceral musculature.

The nerve-endings of the general visceral receptors are generally either simple terminals in the visceral muscles or free arborizations in or under the various mucous surfaces, without the development of specialized accessory cells to form differentiated sense organs. Figure 33 illustrates a sensory ending in the mucous membrane of the esophagus, and Fig. 34 types of nerve-endings upon epithelial cells. The nerve-endings in the visceral muscles are very simple (see Figs. 37 and 38) and the separation of sensory from motor endings here has seldom been effected.

B. Special Visceral Group

22. Organs of Taste.—These are excited by chemical stimulation of taste-buds on the tongue and pharynx by sweet, sour, salty, or bitter

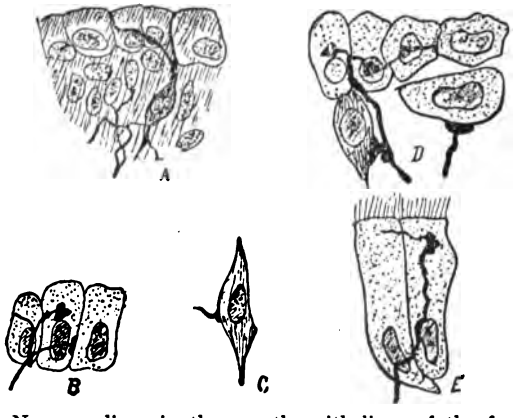

Fig. 34.—Nerve-endings in the mouth epithelium of the frog: *A*, From sensory papilla of the tongue; *B*, cylinder cells; *C*, isolated rod cell; *D*, upper part of papilla; *E*, ciliate cells of palate. (After Bethe, from Wood's Reference Handbook of the Medical Sciences.)

substances. In man this is a strictly interoceptive sense; but in some fishes taste-buds are scattered over the outer body surface in addition

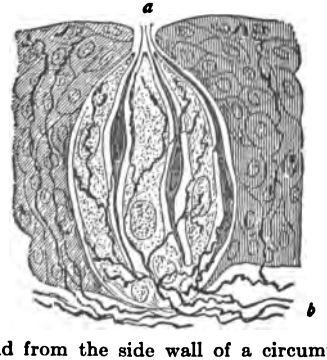

Fig. 35.—Taste-bud from the side wall of a circumvallate papilla of the tongue: *a*, Taste-pore; *b*, nerve-fibers, some of which enter the taste-bud (intragemmal fibers), while others end freely in the surrounding epithelium (perigemmal fibers). (After Merkel-Henle.)

to the mouth cavity, and thus may serve as exteroceptors also. The organ is a flask-shaped collection of specialized epithelial cells of two sorts,

supporting and specific sensory elements (Fig. 35). There is a double innervation, partly by perigemmal fibers whose endings surround the bud, and partly by intragemmal fibers which penetrate the bud and arborize in intimate relation with the specific sensory cells.

23. **Organs of Smell.**—These are excited by chemical stimulation of the specific olfactory mucous membrane of the nose. The number of substances which may act as stimuli is greater than in the case of taste-buds, the number of subjective qualities is also greater, and the discrimination threshold is much lower (see pp. 80 and 244). The peripheral organ of smell is a specific sensory epithelium within the nose. The olfactory epithelium is composed of non-nervous supporting cells and among these the smaller specific olfactory cells. Both kinds of cells extend through-

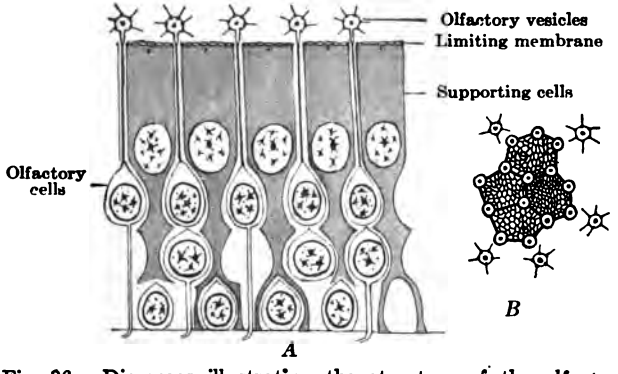

Fig. 36.—Diagrams illustrating the structure of the olfactory mucous membrane of the kitten. *A*, Cross-section. *B*, A section taken tangential to the surface of the epithelium, through the olfactory limiting membrane and showing the rounded openings through which the slender olfactory cells project. The star-shaped structures around the margin of this figure are ciliated olfactory vesicles as seen when looking downward upon the surface of the epithelium at a higher level than the central part of the figure. Drawn by Dr. O. Van der Stricht; for fuller description of these structures, see his paper (1909) cited in the appended bibliography.

out the entire thickness of the sensory epithelium (Fig. 36, *A*) and the olfactory cells are prolonged at the base to form the fibers of the olfactory nerve (Fig. 104, p. 244). This is the only peripheral nerve in the human body whose fibers arise in this way from peripherally placed cell bodies.

The olfactory cells are commonly described as bearing a tuft of cilia at their free ends. The studies of van der Stricht have shown that in the cat the olfactory cells project through openings in the olfactory limiting membrane (which is thus a true fenestrated membrane) and there expand into olfactory vesicles, from which, in turn, the olfactory cilia arise (Fig. 36). The ciliated olfactory vesicles are the true receptors of the sense of smell and embryologically they are derived from the centrosome and its surrounding centrosphere. The olfactory vesicles are embedded in

and supported by an outer semifluid cuticle (not shown in the figure) secreted by the supporting cells.

That the olfactory system was originally an interoceptive sense seems clear; but in all vertebrates living at the present time the visceral responses to smell are less important than the somatic reactions. The sense of smell is the leading exteroceptor in many lower vertebrates, and this function has been secondarily derived from the primary visceral function. We have seen above that the sense of taste in some fishes has secondarily acquired exteroceptive functions; and in the case of smell this secondary change has been carried still further until the exteroceptive function has come to dominate the primitive interoceptive, though the latter has by no means been entirely obliterated.

III. SOMATIC EFFECTORS

24. End-organs on Striated Skeletal Muscles.—This "motor end-plate" is a complex terminal arborization of the motor nerve-fiber, associated with an elevated granular mass of protoplasm and a collection of nuclei of the muscle-fiber (see Fig. 5, *tel*, p. 41).

The somatic muscles whose innervation is here under consideration are derived embryologically from the somites, or primary mesodermal segments of the embryo, while the visceral muscles have a different origin. They are under the direct control of the will and are concerned chiefly with locomotion or other movements which change the relations of the body to its environment. They are typically stimulated to action through the exteroceptive sense organs. They make up the bulk of the musculature of the trunk and limbs and are represented in the head only in the external muscles of the eyeball and a part of the muscles of the tongue.

IV. VISCERAL EFFECTORS

25. End-organs on the Involuntary Visceral Muscles.—These muscles may be unstriated or striated (as in heart muscle). They are innervated through the sympathetic nervous system and typically by a chain of two neurons, the preganglionic and the postganglionic neurons (see p. 258). The body of the preganglionic neuron lies in the central nervous system and its axon passes out into the sympathetic nervous system, where it ends in a sympathetic ganglion. The efferent impulse is here taken up by a postganglionic neuron, whose body lies in the sympathetic ganglion in question and whose axon passes onward through a sympathetic nerve to end in the appropriate effector. The nerve-endings of this system are simple or branched free terminals ending on the surface of the muscle-fiber (Fig. 37); in the case of heart muscle the fibers usually have expanded tips (Fig. 38).

26. End-organs on Glands.—The innervation of these organs is in most respects similar to that of the involuntary muscles last described. A fine plexus of unmyelinated fibers of sympathetic origin envelops the smaller glands and pervades the larger ones; these are believed in some cases to be the excito-glandular fibers.

27. Special Visceral Motor End-organs.—The nerves of these muscles have no connection with the sympathetic nervous system. These effectors are striated muscles which may act under the direct control of the

will. In their evolutionary origin they are derived from the muscles of the gills of the lower vertebrates, and they are developed embryologically from the ventral unsegmented mesoderm and not from the

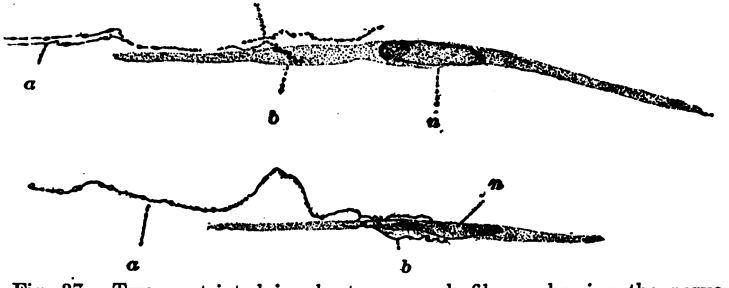

Fig. 37.—Two unstriated involuntary muscle-fibers, showing the nerve-endings: *a*, Axon; *b*, its termination; *n*, nucleus of the smooth muscle cell. (After Huber and DeWitt, from Barker's Nervous System.)

primitive mesodermal segments which give rise to the somatic muscles. They are found only in the head and neck and their nerve-endings are similar to those of the striated muscles of the somatic series. By reason of their anatomical and physiological similarity to typical somatic muscles

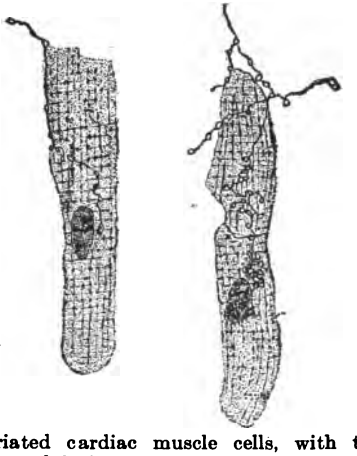

Fig. 38.—Three striated cardiac muscle cells, with their nerve-ending. (After Huber and DeWitt, from Barker's Nervous System.)

they are sometimes called special somatic muscles notwithstanding their kinship phylogenetically and embryologically with the visceral muscles. They are of mixed nature and either usage is necessarily a compromise.

Summary.—We have seen that the chief function of the sense organs is to lower the threshold of excitability of the body in definite places to particular kinds of stimulation, and thus to effect an analysis of the forces of nature so far as these concern the welfare of the body. The nature of this analysis of the environing energy complex was illustrated by a review of the ways in which the body may respond to different kinds of vibrations. The senses, as this word is commonly used, were distinguished by four criteria, termed briefly the psychological, physical, anatomical, and physiological. Then followed a physiological classification of the receptors and effectors of the human body.

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CHAPTER VI

THE GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM

THE functions of the body are generally effected by chemical changes within its protoplasm. These chemical changes in the aggregate we term "metabolism" and they generally involve a rather slow interchange of the chemical substances of food and waste materials between the cytoplasm and the lymph which surrounds the cells and between the cytoplasm and the protoplasm of the nucleus (karyoplasm). The rate of metabolism is dependent upon many factors, one of which is the time required for the passage of soluble substances through the cell membrane and through the nuclear membrane which separates the cytoplasm from the karyoplasm.

In the nerve-cells both of these sorts of chemical interchange are facilitated by the form and internal structure of the cell. As we have already seen (p. 42), the widely branching dendrites present a large surface for the absorption of food materials from the surrounding lymph and the elimination of waste. The specific nervous functions involve the consumption of living substance, both in the cell body and in the nerve-fibers. This is in part an oxidation process, and this phase of the activity can be roughly measured by the amount of carbon dioxid eliminated. Until very recently it was not possible to secure any evidence of CO_2 production in nerve-fibers; in view of this and of the further fact that nerve-fibers seem to be less susceptible to fatigue than nerve-cells and synapses, many physiologists assumed that nervous conduction is not a chemical process, but perhaps some sort of molecular vibration. The conduction of a nervous impulse through a living nerve-fiber is accompanied by an electric change, the so-called negative variation, or action current, which by some physiologists has been identified with the nervous impulse itself. This and other complicated theories of nervous transmission assume that the process is essentially a physical change (prob-

ably of an electric nature) which involves no chemical alterations, no consumption of material, no metabolism.

But by means of recently devised apparatus of extreme delicacy Tashiro has shown very clearly and quantitatively that the resting nerve-fiber eliminates CO_2 and that during functional activity caused by stimulation the amount of CO_2 is increased to about double that of the resting nerve. The same investigator subsequently showed that the amount of CO_2 given off by nerve-fibers is quite as great per unit of weight as that given off by the nerve-cell bodies of the ganglia. Tashiro has shown, moreover, that the rate of CO_2 production is greater in that portion of a nerve-fiber which lies nearer to the source of the stimulus than in a similar portion of the same nerve-fiber farther from the receptive end and nearer to the discharging end. This applies to both sensory and motor fibers. Child has confirmed this by showing that different parts of the nerve-fiber show differences in susceptibility to certain poisons corresponding to the differences in rate of oxidation of their substance. There is, accordingly, a physiological gradient in the nerve-fiber, the physiological activity diminishing in the direction of the normal conduction of the nervous impulse. The neuron is thus seen to have an intrinsic physiological polarity of its own quite apart from that occasioned by the irreversible character of the synapse (see p. 55).

R. S. Lillie, in an extensive series of experiments, has presented some very instructive analogies between certain phenomena of electrolysis and autocatalysis and protoplasmic conduction, and he has developed a theory of nervous conduction which unites the biochemic and bio-electric phenomena in a series of self-propagating cycles. He has been able in inorganic electrolytic processes to simulate nervous conduction very closely and to vary the rate of transmission at will. These theories are discussed, with citations of literature, by Child (1921, p. 70).

In the unmyelinated nerves of vertebrates the rate of progression of the nerve impulse varies from 0.2 to 8 meters per second; in the myelinated sciatic nerve of the frog it varies from 24 to 38 meters per second; and in human myelinated nerves it may be as rapid as 125 meters per second. This rate

of conduction of the nervous impulse in peripheral nerves varies greatly with different animals, with different nerves in the same animal, and in the same nerve under different physiological conditions.

The *reaction time* required for the performance of various reflex acts can be very accurately measured, and it is found that the time of even the simplest reflex is considerably greater than is required for the transmission of the nervous impulse through the conductors involved. The average rate of conduction in human nerves is probably about 120 meters per second, and the simplest reaction times which have been measured in psychological laboratories vary between 0.1 and 0.2 second (from 0.117 to 0.188 for reactions to touch, and from 0.120 to 0.182 for reactions to sound). The total time required for transmission of the nervous impulse through the nerve-fibers involved in these reactions need not exceed 0.02 second, whence it appears that the greater part of the reaction time is otherwise consumed. A part of this excess time is required to overcome the inertia of the end-organs (receptor and effector), and the remainder is used in the central nervous system. This "central pause" is characteristic of all reflexes and, in fact, has a profound significance in connection with the evolution of the higher associational functions of the brain. The introduction of further complexity in the reaction, of whatever sort, usually lengthens the time of the central pause, though long training in making a discriminative reaction may reduce this pause almost to the time of a simple reaction.

Many attempts have been made to determine the central time of reactions of different degrees of complexity by subtracting from the total time in each case the probable time required for the peripheral processes and by subtracting the total time required for the simpler reactions from the total time taken in more complex discriminative reactions. But further analysis (particularly more critical introspection) has shown that in these human reactions the problem is too complex to be resolved by this method (see Ladd and Woodworth, 1911, p. 497).

The simpler reflexes of lower vertebrates can be studied physiologically, and these give data which are much more readily analyzed than the more complex human reactions. In the case of the simplest reflex obtainable in the spinal cord of the frog, the central pause was estimated by Wundt to be only 0.008 second, *i. e.*, all of the time required for the reaction except this interval was used in the peripheral apparatus. But in a crossed reflex, where the reaction occurs on the opposite side of the body from the stimulus, the increased complexity of the central process consumed 0.004 second additional.

Miss Buchanan (1908), with more accurate methods of study, finds in the frog that the central time varies between .014 and .021 second. She also measured the additional latent time required for a crossed reflex, and found it to be of the same order of magnitude as the latent time of the simple reflex (instead of half as much as in Wundt's experiments), that is, the crossed reflex required about twice the latent time in the spinal cord as the uncrossed reflex. It is assumed that this central pause in the uncrossed reflex is consumed chiefly in the synapses between the peripheral sensory and the peripheral motor neurons, and that only one such synapse is involved in each simple reflex connection (a two-neuron circuit, see Fig. 1, p. 26); but in the crossed reflex two such synapses are

involved (a three-neuron circuit such as the pathway from *d.r.*2 to *v.r.*1′ through *correlation neuron* 1 in Fig. 61, p. 144), and the introduction of the second synapse doubles the time. It is, therefore, assumed that it requires in the frog between .01 and .02 second for the nervous impulse to pass the synapse between two neurons in a reflex circuit.

Turning now to the activities of the nerve-cell body, it will be recalled (p. 47) that here the chromophilic substance is generally distributed throughout the cytoplasm. This substance is very similar to that of the chromatin of the nucleus, from which it is said to be derived during the development and functional activity of the neuron. During the resting state of the cell it and other reserve materials accumulate in the cytoplasm; and now, when the cell is stimulated to activity, the energy thus stored up may be liberated almost instantly because the chemical substances necessary for the reaction are widely diffused throughout the entire mass of the cytoplasm.

The function of neurons, as compared with that of most other cells of the body, may, therefore, be described as of the explosive type. A word of explanation will render the analogy clear. In ordinary combustion, oxygen is supplied to the surface of the burning material, say a blazing log, and the chemical process of burning goes on only as fast as the superficial parts can be oxidized and removed. But explosive substances are chemically so constituted that as soon as combustion begins oxygen is liberated in the interior of the material and the process of oxidation takes place almost instantaneously throughout the entire mass. Similarly in the nerve-cell, the processes of metabolism are not dependent upon the slow interchange of substances through the nuclear membrane between the cytoplasm and the nuclear plasm; but the chromophilic substance distributed through the cytoplasm permits of much more rapid responses. The organization of the protoplasm of the nerve-cell is such that a very small stimulus may liberate a large amount of energy with explosive suddenness. The energy thus liberated does not all leave the cell, but part of it is directed into the axon, which is thereby excited to conduct a nervous impulse to the appropriate end-organ or to the next synapse, and thence to a second neuron.

The conduction of nervous impulses within the central nervous system in some cases takes place through well-defined and

insulated bundles of fibers, which are termed *tracts;* but in most cases there is more or less complexity introduced by collateral avenues of discharge to other specific centers, as in the complex forms of reflex systems described in Chapter IV, or by a more diffuse type of irradiation (p. 69). The organization of the central nervous system is such that in general the excitation of any peripheral sensory neuron may be transmitted to very di-

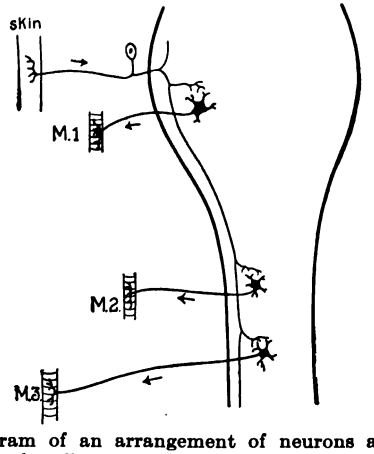

Fig. 39.—Diagram of an arrangement of neurons adapted for the distribution of a single afferent nervous impulse to several different motor organs.

verse and remote parts of the brain, each of which may call forth its own characteristic form of response.

The physiological effects of such a dispersal of an incoming nervous impulse within the central nervous system may be very different, depending on the connections of the pathways which are taken by the neurons of the second order. If these pathways diverge so that the stimulus is distributed among several different effector systems, this would tend to disperse the energy of the afferent impulse and a relatively strong stimulus is necessary to call forth a response. This is the situation in case a painful prick on the skin of the face calls forth reflex movements of, say (1) twitching of the facial muscles; (2) turning the head away, and (3) a movement of the hand to remove the irritant. Here the stimulus arising at a single point in the skin (Fig. 39) is distributed to three widely separated motor centers (*M*.1, *M*.2, *M*.3). On the other hand, in case the stimulus received by the neuron of the first order is distributed to several neurons, all of which discharge into the same motor center, the stimulus may be reinforced because each neuron of the second order may discharge its own reserve energy in such a way as to send out a stronger

impulse than the one received, so that the total discharge into the motor center is greatly strengthened (Fig. 40). Such an impulse may be said to accumulate momentum as it advances like an avalanche on a mountain slope, and hence this type of reaction has been termed by Ramón y Cajal "avalanche conduction." In some parts of the brain there are very special mechanisms for this sort of cumulative discharge, as in the cortex of the cerebellum (p. 214) and the olfactory bulb (p. 244).

The intensity of nervous discharge in all of its forms is very dependent upon the general physiological state of the body, some conditions, such

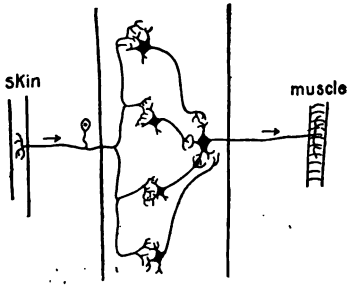

Fig. 40.—Diagram of the mechanism of reinforcement whereby a single weak afferent nervous impulse may be received by several neurons of the second order which discharge their greatly strengthened nervous impulses into a single final common path.

as fatigue and various intoxications, tending to depress the activity, and other conditions tending to facilitate it. The maintenance of good nervous tone is, therefore, essential to the highest efficiency. Some of these physiological agents may also act locally on particular parts of the nervous system and thus determine the selection of one instead of another out of several possible modes of response in the variable type of behavior.

Fatigue of nerve-cells may be brought about in two ways, which have been clearly distinguished by Verworn: (1) by the consumption of reserve material from which the energy of the cell is derived more rapidly than this material can be restored, and (2) by the accumulation of waste-products more rapidly than they can be eliminated from the cell. These forms of fatigue have recently been named by Dolley respectively "fatigue of excitation" and "fatigue of depression."

In his interesting discussion of neuro-muscular fatigue, Stiles (1914, p. 101) enumerates several particular ways (in addition to the two general methods just mentioned) by which fatigue may be brought about, among which are the following: (1) fatigue of muscle-fibers, (2) fatigue of the junction of the motor

nerve with the muscle-fiber at the motor end-plate (see Fig. 5, p. 41), (3) fatigue of the nerve-fibers, (4) fatigue of the motor nerve-cells, (5) fatigue of the synapses between the nerve-cells, (6) fatigue of the sense organs and afferent apparatus, (7) fatigue of the centers of voluntary control. The first, second, fourth, and fifth types commonly play a part in ordinary fatigue, the third is insignificant, and the sixth and seventh may be present. The synapses and the motor end-plates are probably especially susceptible to fatigue of depression by toxic substances, and the muscle-fibers and nerve-cell bodies to fatigue of excitation by consumption of their material.

A resting neuron when excited to activity at first increases in size by reason of the stimulus given to general metabolic activity. The first signs of fatigue result from the exhaustion of the oxygen supply of the cells; then follows the consumption of the reserve food materials, chiefly those represented in the chromophilic substance, with consequent shrinkage of the Nissl bodies, as these are seen in stained preparations. In extreme fatigue the ultimate dissolution and death of the cell may be hastened by the accumulation of toxic products of cell metabolism.

It appears to be well established by numerous experimental studies that at the beginning of functional activity both the nucleus and the cytoplasm of the resting neuron are enlarged, and that with the onset of fatigue there is a shrinkage, especially of the nucleus, with vacuolation of the cytoplasm and solution of the Nissl bodies due to the consumption of the chromophilic substance during activity. The neurofibrils are also said to be modified during functional activity. After excessive activity they become more slender and apparently increase in number, while during rest and after hibernation of those animals which have this habit the neurofibrils become thicker and less numerous.

Cells whose chromophilic substance has been consumed by active function may after rest return to the normal form; but if the excitation be carried beyond the stage of normal fatigue, recovery of the neuron is impossible and it gradually disintegrates, resulting in the permanent enfeeblement of the nervous system.

The observations of Dolley have suggested to him that the volume of the nucleus bears a constant relation to the volume of the cytoplasm in all resting nerve-cells of the same type. In varying functional states of excitation and depression this mass relation is disturbed in accordance with the formula: Activity finally results in a disturbance of the normal nucleus-cytoplasmic relation in favor of the cytoplasm (fatigue of excitation), while depression resulting from accumulated toxins finally results in a disturbance of this relation in favor of the nucleus. In short, the depression of the neuron by any form of intoxication or otherwise gives the converse picture of structural changes from that presented by fatigue of excitation.

Most of the physiological work which has been done upon fatigue has been directed toward the isolation of special toxic substances such as in Dolley's scheme would produce "fatigue of depression." It has been shown that prolonged muscular exertion produces toxins (carbon dioxid, lactic acid, and others) which are dissolved in the blood and exert a profound depressing influence upon all of the tissues of the body. If the blood of a fatigued animal be injected into or transfused with a perfectly fresh animal of the same species, the latter immediately manifests all the signs of fatigue.

It is often taught that a change of work is physiologically equivalent to complete rest. It is true that, so long as one is well within the limits of extreme fatigue, a change of work will prolong efficiency far beyond that which would be possible in continuous activity of a single nervous or muscular mechanism. Some experiments show that mental efficiency is greatly impaired in extreme muscular fatigue, and, conversely, muscular power is greatly weakened after long sustained mental work. But the results of various experiments to test these points are conflicting and ambiguous, and the problem is one of great complexity. Glandular secretions are also apparently often reduced in extreme fatigue, thus, for instance, reducing the efficiency of the digestive organs. These effects are doubtless due to the accumulation of toxic products in the blood, producing a true "fatigue of depression" throughout the entire body.

It has been suggested that the local feelings of muscular fatigue are due to excitations of the organs of the muscular sense in the muscle spindles (p. 92); but the evidence for this does not seem very convincing.

The experiments of Dolley suggest to him, further, that the more highly differentiated nerve-centers are more susceptible to the structural alterations of fatigue than are those of the lower reflex systems. It is a well-known fact that sustained mental work produces the subjective evidences of fatigue more promptly than does muscular work, and that during severe mental training one is more apt to go "stale" than during physical training. This principle has been widely recognized in the provision of short working hours and frequent holidays for pupils and teachers in our schools; it should be still further extended, especially in commercial and professional life. Its neglect is in large measure responsible for the prevalence of various forms of nervous breakdown.

The early fatigue of the higher voluntary centers is particularly evident in young children, where continuous sustained attention is impossible except for very short periods. By training, these periods can be greatly lengthened, the nervous mechanism involved here probably being the acquisition of a wider range of associations related with the subject which occupies the focus of attention, so that individual neurons or systems of neurons which participate in the functional complex may be temporarily rested while other related systems are brought into maximum activity, without thereby interrupting the continuous progress of the train of thought.

The neurological basis of *sleep* is obscure, though the physiological phenomena seem to be in many respects analogous with those of fatigue. Of the various theories which have been suggested, one which has perhaps excited greatest interest is the belief that some soluble toxin is produced during waking hours which induces sleep by a process similar to that of the "fatigue

of depression." Legendre and Piéron (1911) have performed instructive experiments on dogs regarding the source and nature of the toxic substances supposed to cause sleep. Such a substance is present in the cerebrospinal fluid of fatigued animals and in less amount in the blood-serum and is probably of cerebral origin. The injection of these fluids from somnolent animals into fresh ones induces sleep and causes structural alterations in the nerve-cells of the cerebral cortex of the frontal lobes.

Many physiological experiments seem to show that, though the predisposition to sleep may be brought about by the accumulation of toxins in the blood or by other general causes, the actual falling asleep is due to some other factor. Fatigue of the vasomotor center has been suggested as the real physiological cause of sleep.

The doctrine of the retraction of the neuron was a popular view several years ago. This teaches that during sleep (and according to some authors in less measure during fatigue also) the dendrites of the neurons retract toward their cell bodies and away from contact with the axons of other neurons with which they are in synaptic union, thus increasing the resistance to nervous conduction at the synapse; but there is no satisfactory evidence that this occurs.

The view formerly prevalent that sleep is due to cerebral anemia seems to have been disproved by the careful experiments of Shepard on the volume of the brain during waking and sleeping conditions. The blood supply sent to the brain was measured by studying the volume of the brain in two men whose skulls had been trephined. In these cases there was a marked increase of the volume of the brain during sleep, the increase being at its maximum from 15 to 25 minutes after the subject fell asleep, and thereafter diminishing somewhat, though always remaining greater during sleep than when awake.

The numerous theories regarding the neurological processes taking place in the cerebral cortex during the progress of such mental functions as attention, association of ideas, etc., are likewise as yet entirely unproved. It has been suggested that during cerebral function the resistance of some pathways may be diminished by the ameboid outgrowths of the dendrites so as to effect more intimate synaptic union with the physio-

logically related neurons, while the resistance of other paths may be increased by the retraction of dendrites from their synapses. Others believe that the neuroglia may participate in the process by thrusting out ameboid processes between the nervous terminals in the synapses and thus increasing the resistance. Lugaro has suggested a different interpretation, in accordance with which during sleep there is a generally diffused extension of all nervous processes, thus providing for the uniform diffusion of incoming stimuli, while in the state of attention all of these processes retract save those which are directed in some definite direction, thus narrowing the stream of nervous discharge so as to intensify it and direct it into the appropriate centers. There is no direct evidence for any of these theories, and the scientifically correct attitude toward them is frankly to admit that at present we do not know what physiological processes are involved in any of these functions.

Chemotaxis.—The development and evolution of the brain suggest many physiological questions which are still far from satisfactory solution. It has often been asked, for instance, how the nerve-fibers which arise from cell bodies in one part of the nervous system find their way through long and often devious courses to remote parts and there effect physiological relations with the appropriate centers necessary for establishing useful reflexes. Similarly the peripheral nerves are known to grow outward toward their respective areas of distribution and one wonders how they find their way and are able to reach the proper end-organ. Numerous observations and experiments show that this is not a matter of chance, but that the nerves appear to seek out their appropriate end-organs.

This problem is very complex and doubtless many factors operate. Among these is probably the familiar biological principle of chemotaxis. Many organisms or parts of organisms grow toward certain specific kinds of chemical emanations; thus, plant roots in the soil will grow toward water. This movement is called chemotaxis and it has been assumed that a similar manifestation of biochemical affinity is operative in the developing nervous system (see Ramón y Cajal, Système Nerveux, vol. i, p. 657).

Many organs of the adult body are known to secrete specific soluble chemical substances termed hormones, which diffuse throughout the lymph or blood and call forth functional activity in remote organs (see p. 251) It is possible that during development of the body the organs, as soon as definite stages of growth are reached, secrete similar substances which diffuse through the surrounding tissue and each of which has a chemotactic affinity for a certain type of developing neurons. Thus, the developing muscles may secrete a substance to which the motor neurons of the spinal cord react by a growth of their embryonic axones toward the source of the stimulating material.

Neurobiotaxis.—In the course of the evolution of the vertebrate nervous system numerous groups of cell bodies ("nuclei") with specific

functions have moved from their primitive positions to new locations. This is quite a different thing from the chemotactic outgrowth of nerve fibers described above. Many of these phylogenetic migrations of nerve-cell bodies have been accurately described by Kappers and his school and are ascribed to a factor termed neurobiotaxis. This principle is that in the course of phylogeny cell bodies tend to migrate in the direction from which they habitually receive their stimuli; *i. e.*, in the direction taken by their dendrites. If there is a change in the direction from which a given nucleus receives its chief stimuli, the nucleus as a whole will tend to move toward the new source of excitation and away from the old. Many illustrations are given in the papers by Kappers and Black and the works there cited.

This shortening of the dendrites is doubtless due in part to the fact that these processes of the neuron are structurally less perfectly adapted to transmit nervous impulses than are the axons (see p. 41). In this connection it is interesting to recall that the neurons of the spinal and cranial ganglia, which do not exhibit neurobiotactic migrations, have long dendrites whose structure is similar to that of their axons and are presumably equally good conductors. But other factors also appear to be present which are reviewed by Kappers (1917) and these seem to him to be related with the electrical phenomena of nervous conduction (galvanotaxis). These factors have also been critically analyzed by Child (1921) in connection with a detailed discussion of the general physiology and bioelectrics of the differentiation of nervous tissues.

Summary.—The forms assumed by neurons are shaped in part by their nutritive requirements and in part by their functional connections. The metabolism of nervous protoplasm, as measured by its CO_2 output, is found to be as active in nerve-fibers as in the cell bodies. In a nerve-fiber the metabolic activity is found to be greatly increased during the transmission of a nervous impulse; and nervous conduction evidently involves a chemical change in the conducting fiber. The rate of transmission of a nervous impulse depends on the structure and physiological state of the nerve-fiber involved. The metabolic activity of the nerve-cells is of a very different sort from that of nerve-fibers, and may be characterized as of the explosive type. There are at least two factors involved in the fatigue of the nervous system: (1) fatigue of excitation, resulting from the consumption of the materials of its protoplasm, and (2) fatigue of depression, resulting from the accumulation of toxic products of cellular activity. Each of these processes produces its own very special series of morphological changes in the neurons. The neurological functions involved in sleep and the higher mental processes are as yet unknown.

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CHAPTER VII

THE GENERAL ANATOMY AND SUBDIVISION OF THE NERVOUS SYSTEM

On merely topographic grounds the nervous organs are divided into the *central nervous system*, or axial nervous system, comprising the brain and spinal cord, and the *peripheral nervous system*, including the cranial and spinal nerves, their ganglia and peripheral end-organs, and the sympathetic nervous system. The nerves are simply conductors, putting the end-organs into physiological connection with their respective centers. The general form of the human central nervous system and its connections with the peripheral nerves are seen in Fig. 41. The nerves connected with the spinal cord are the spinal nerves, those connected with the brain are the cranial or cerebral nerves, and both of these systems of nerves together are called the cerebrospinal nerves, in contrast with the sympathetic nerves, which latter may or may not be connected with the central nervous system (see p. 251).

The central nervous system is the great organ of correlation and integration of bodily processes. Its primitive form in vertebrates is a simple tube, and this is the form shown in an early human embryo (see Fig. 46, p. 124). The original tubular form is but little modified in the trunk region of all vertebrates, where the spinal cord (medulla spinalis) is formed by a tolerably uniform thickening of the lateral walls of the tube (see Figs. 41, 58). But in the head region the brain (encephalon) is formed by the very unequal thickening of different parts of the walls of the tube and by various foldings brought about thereby. The general arrangement of the human central nervous system at successive stages of development is seen in Figs. 47–51.

The external form of the brain has been shaped by the space requirements of the nerve-cells and fibers which make up its

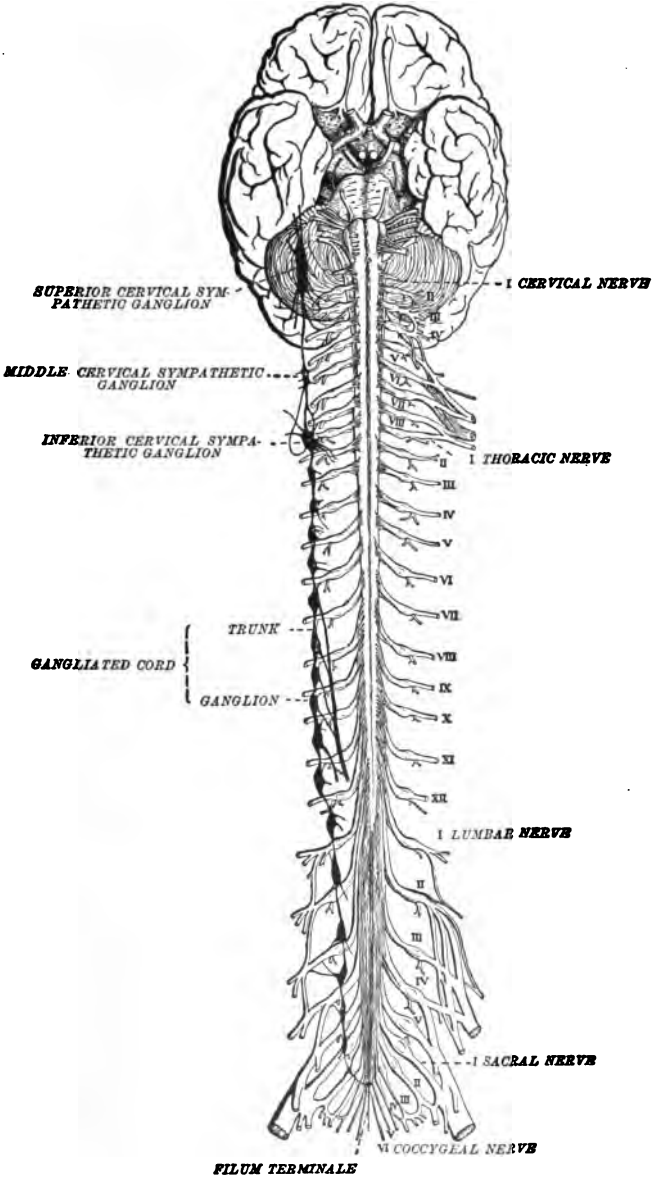

Fig. 41.—The human central nervous system from the ventral side, illustrating also its connections with the cerebro-spinal nerves and with the sympathetic nervous system, the latter drawn in black. (After Allen Thompson and Rauber, from Morris' Anatomy.)

substance. A group of nerve-cells which performs a single function is often spoken of as the "center" of that function; but it should be borne in mind that this does not imply that this function resides exclusively in that place. These functions are all more or less complex and the "center" is usually the region where various nervous impulses are received and redistributed; it is, therefore, roughly analogous with the switchboard of an electric plant.

The nerve-fibers which conduct nervous impulses toward a given center are called *afferent*, and those which conduct away from the center are called *efferent* with reference to that center. Most of the peripheral nerves are mixed, in the sense that they carry both afferent and efferent fibers with reference to the central nervous system. The efferent fibers may excite movement in muscles (motor fibers) or secretion in glands (excito-glandular fibers); other efferent fibers which check the action of the organ to which they are distributed are called inhibitory fibers. The afferent fibers of the peripheral nerves are often called sensory fibers, though it must be borne in mind that their excitation is not always followed by sensations or other conscious processes.

The vertebrate nervous system when examined in the fresh condition is found to be made up of white matter (substantia alba) and gray matter (substantia grisea), the white matter containing chiefly nerve-fibers with myelin sheaths (see p. 49) and the gray matter nerve-cell bodies and unmyelinated fibers. The centers are, therefore, generally gray in color and the intervening parts of the central nervous system are white.

A group of nerve-cells constituting a center as above described is often called a "nucleus," a term which has nothing to do with the nuclei of the individual cells (see p. 40) of which the center is composed. Some critical writers use the word "nidulus" (originally suggested by C. L. Herrick) or "nidus" (Spitzka) for such a center, thus avoiding the ambiguity in the use of the word nucleus. The term "ganglion" is also sometimes used for nuclei or centers within the brain (ganglion habenulæ, ganglion interpedunculare, etc.), but this usage is objectionable, for the use of the word ganglion in vertebrate neurology should be restricted to collections of neurons outside the central nervous system, such as the ganglia of the cranial and spinal nerves and the sympathetic ganglia.

A nucleus from which nerve-fibers arise for conduction to some remote

part of the nervous system is called the *nucleus of origin* of these fibers; conversely, a nucleus into which nervous impulses are discharged by fibers arising elsewhere is the *terminal nucleus* of those fibers. Any correlation center is, therefore, a terminal nucleus for its afferent fibers and a nucleus of origin for its efferent fibers.

The centers or nuclei within the brain are of two general sorts: (1) primary centers and (2) centers of adjustment. The second class includes centers of correlation and coördination (p. 36). The primary centers are directly connected with peripheral nerves, either as terminal nuclei of afferent fibers or as nuclei of origin of efferent fibers (see pp. 44, 116). The elements out of which most acts are compounded are reflexes (see p. 59), and in the simplest of these reflexes a sensory nervous impulse received from the periphery by a terminal nucleus may be passed on to a nucleus of origin and thence directly to the organ of response; but in more complex reflexes the incoming nervous impulse is first transmitted from the terminal nucleus to a correlation center, where it may meet other types of sensory impulses and then be discharged into any one of several possible motor pathways. For illustrations of these types of connection see Chapter IV.

In general, ganglia or nerve-centers are interpolated in conduction pathways only where some complication of the reaction is to be provided. The conduction path is usually here interrupted by synapses and various forms of correlation or coördination mechanisms are present (see p. 36 and Chapter IV). Many of the sympathetic ganglia provide the mechanism for local reflexes in which the central nervous system does not participate (p. 252). The spinal ganglia (see Fig. 1, p. 26) are often regarded as merely trophic centers for the maintenance of the fibers of the peripheral nerves; but they evidently have functions of correlation in addition to this, for numerous synapses between sympathetic and cerebro-spinal neurons occur here (see p. 256 and Fig. 109) which play a part in the correlation of visceral and somatic reactions.

The primary centers and the simpler adjusting centers of the brain can be studied much more readily in the brains of fishes, which lack the cerebral cortex whose enormous development in the human brain has obscured the relations and connections of

the more primitive reflex apparatus. Figures 42, 43, and 44 illustrate the relations of the principal sense organs to the brain in a small shark, the common marine dogfish. Figures 42 and 43 (on the right side) illustrate the arrangement of the principal roots and branches of the cranial nerves. On the left side of Fig. 43 the relations of the nose, the eye, and the ear to

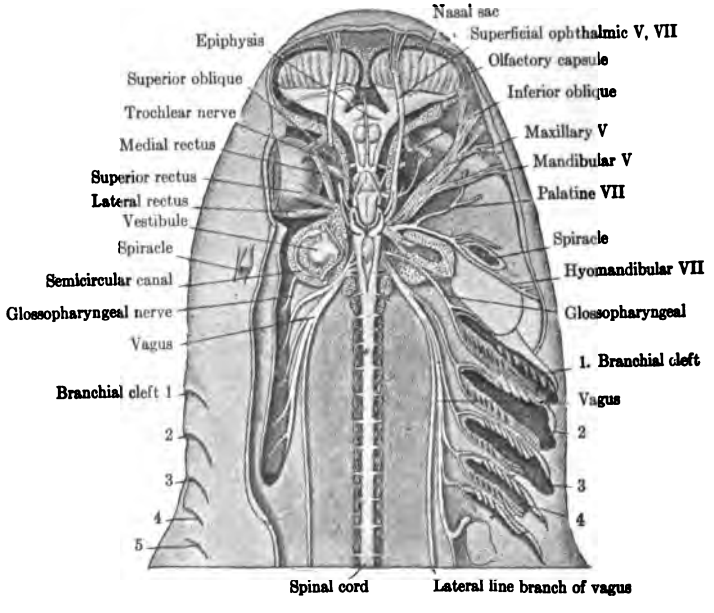

Fig. 42.—Dissection of the brain and cranial nerves of the dogfish, Scyllium catulus. The right eye has been removed. The cut surfaces of the cartilaginous skull and spinal column are dotted. (After Marshall and Hurst, from Ranson's Anatomy of the Nervous System.)

the brain are indicated; and Fig. 44 shows a side view of the brain and the sensory roots of the cranial nerves.

In fishes there is a system of small sensory canals widely distributed under the skin. These contain sense organs somewhat similar to those in the semicircular canals of the internal ear, and their functions are probably intermediate between those of the organs of touch in the skin and those of the internal

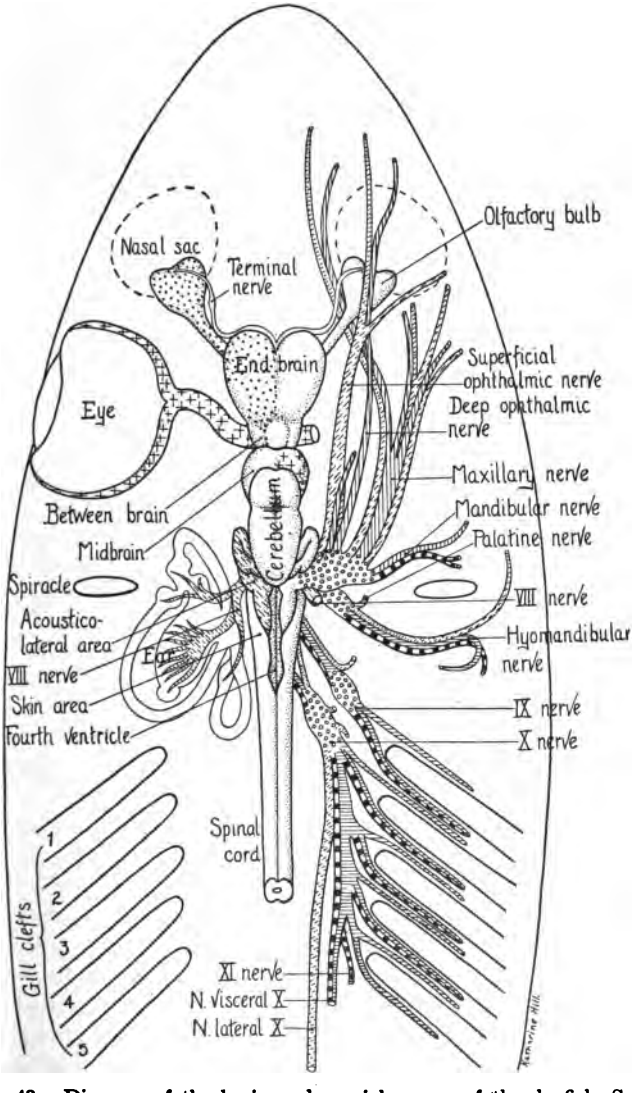

Fig. 43.—Diagram of the brain and cranial nerves of the dogfish, Squalus acanthias, from above. Natural size. The Roman numerals refer to the cranial nerves. The olfactory part of the brain is marked with coarse dots, the visual apparatus with crosses, the acoustico-lateral nerves and centers with broken oblique lines, the visceral sensory nerves with horizontal lines, the general cutaneous nerves with vertical lines, and the visceral motor nerves with black and white rectangles.

ear, responding to water vibrations of slow frequency and probably assisting in the orientation of the body in space. These are the lateral line canals. They are innervated by special roots of the VII and X pairs of cranial nerves (the lateralis roots of these nerves, Figs. 43 and 44). The lateral line organs and their nerves are entirely absent in higher vertebrates (see p. 224).

For a fuller account of the nervous system of the dogfish, with more detailed drawings of the components of the cranial nerves, see Herrick and Crosby (1920, pp. 16–38).

The lateral line nerves and the acoustic nerve (VIII pair) in fishes terminate in a common center within the brain (the

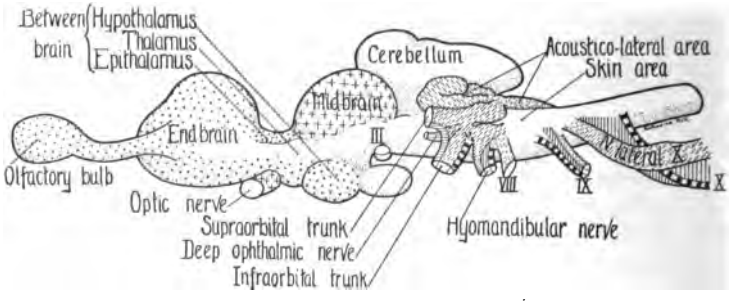

Fig. 44.—The brain of Squalus acanthias from the left side. Designations of nerve roots and brain centers the same as in Fig. 43. Compare Fig. 68, p. 166.

acoustico-lateral area), which is shaded with oblique cross-hatching in Figs. 43, 44, and 68. The nerves of general cutaneous sensibility also terminate in a particular region which is marked "skin area." The visceral nerves from the gills, stomach, etc., all enter a single "visceral sensory area," which is shaded with horizontal lines in Fig. 68, p. 166. The eye is also connected with a special region in the "midbrain," the optic lobe, which is marked with crosses; and the nose is connected with a part of the forebrain which is stippled.

We may, therefore, recognize in this fish a "nose brain," an "eye brain," an "ear brain," a "visceral brain," and a "skin brain," each of these peripheral organs having enlarged

primary terminal nuclei which make up definite parts of the brain substance. Remembering that the primitive brain was a simple tubular structure, we observe that each one of the chief sense organs and each group of similar sense organs sends sensory nerves inward to terminate in a special part of the wall of the primitive neural tube, and that here a thickening of the wall of the tube has taken place to provide space for the appropriate terminal nucleus. It may be noticed, further, that all of these structures (except a part of the olfactory centers) lie in the dorsal part of the brain. An examination of the primary motor centers would show that they are distributed in a somewhat similar fashion along the ventral part of the brain.

The facts just recounted give a clear picture of the pattern of functional localization of the primary reflex centers in a simple type of brain, and they show that all of the more obvious parts of this brain except the cerebellum are in simple direct relation with particular peripheral organs. In other words, nearly the whole of this brain is directly concerned with simple reflexes and (aside from the cerebellum) no large centers for the higher types of adjustments are present. The primary reflex centers are found to be arranged in accordance with essentially the same pattern in the human and all other higher brains, though in these cases the pattern is modified and much obscured by the presence of greatly enlarged correlation centers, of which the cerebral cortex is the chief. The structure and significance of the cerebral cortex form the theme of the last three chapters of this work.

The central nervous system of the earliest vertebrates was probably a simple longitudinal tube of nervous tissue with which the peripheral nerves were connected in a segmental fashion (see p. 31). This is the permanent form of the spinal cord and its nerves in all vertebrates (see p. 135 and Fig. 41). In the brain the enlargement of the primary reflex centers and of the correlation centers directly related to them has changed the form of the tube and disturbed the primitive segmental arrangement of the cranial nerves, as is indicated in Figs. 43 and 44. Nevertheless, this more ancient part of the brain is sometimes called the *segmental apparatus*, to distinguish it

from two very large coördination and correlation mechanisms which are of later evolutionary origin, namely, the cerebellar cortex and the cerebral cortex, which are termed *suprasegmental* structures (A. Meyer).

The segmental apparatus of even the lowest vertebrates shows the regional differentiation suggested in Figs. 43 and 44, each of these regions being elaborated in correspondence with the particular type of end-apparatus in connection with it.

In addition to these particular centers of reflex correlation, there are provided higher centers for the integration of all activities of the body as a whole (see p. 37). In lower vertebrates this integration is very simply manifested, each part of the central nervous system possessing much more complete autonomy than is the case in man (cf. Herrick and Coghill cited on pp. 71, 199). As we pass from lower to higher vertebrates the chief integrating center shifts its position from the midbrain in fishes to the thalamus and corpus striatum complex in reptiles and birds, and finally to the cerebral cortex in mammals. These integrating centers increase in size and functional importance as their anatomical plane is moved further away from the primary reflex centers in the brain stem, until finally in the cerebral cortex they are completely emancipated from control by any particular reflex systems but instead they themselves may regulate all bodily activities.

The segmental apparatus is often called the *brain stem.* It includes practically all of the fish brain (Figs. 43 and 44) except the cerebellum, for in these animals there is no cerebral cortex. If in the human brain we dissect away the cerebral cortex and the cerebellar cortex and the white matter immediately connected therewith we have the form shown in Fig. 45. This is the human brain stem.

Cortical Dependencies.—It should be noted that in man the brain stem is not exactly synonymous with the segmental apparatus, for the human brain stem includes many parts which have been developed to facilitate the functional interaction between the cortex and the phylogenetically older reflex centers. These structures which are functionally subsidiary to the cortex are called cortical dependencies (see pp. 238, 294). The brain stem contains similar dependencies of the cerebellum (pons, red nucleus, etc.).

The cerebellum appears in the evolutionary history of the vertebrate brain much earlier than the cerebral cortex; its functions are wholly reflex and unconscious (see pp. 172, 205) and are concerned chiefly with motor coördination, equilibration, and, in general, the orientation of the body and its members in space. Its activities are of the invariable, innate, structurally predetermined type (see pp. 22, 32, 84). The cerebral cortex, on the other hand, is the organ of the highest

and most plastic correlations, which are in large measure individually acquired. It attains its maximum size in the human brain.

In recognition of the late phylogenetic origin of the cerebral cortex Edinger has called the brain stem (with the exception

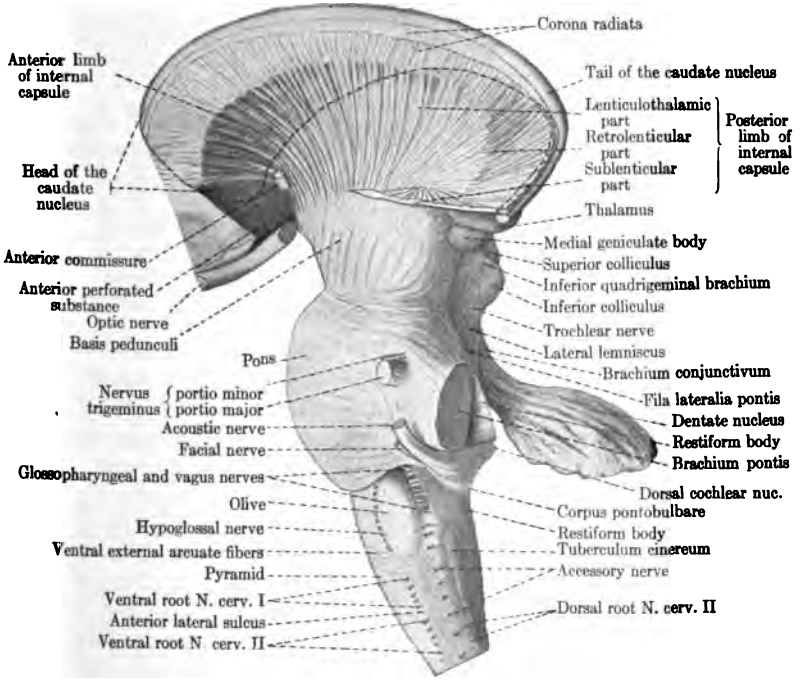

Fig. 45.—Lateral view of the human brain stem. (From Ranson's Anatomy of the Nervous System.)

of the cortical dependencies) and cerebellum the old brain (palæëncephalon), and the cerebral cortex and parts of the brain developed in relation therewith the new brain (neëncephalon).

The terminology of the brain is in great confusion. Most of the more obvious parts were named before their functions were known, the same part often receiving many different names,

and sometimes the same name being applied to very different parts. To remedy this situation the German Anatomical Society in 1895 published an official list of anatomical terms which is known as the Basle Nomina Anatomica (commonly abbreviated as B. N. A.). Each of these terms has a clearly defined significance and they are now very widely used, though many anatomists continue to use some older and un-

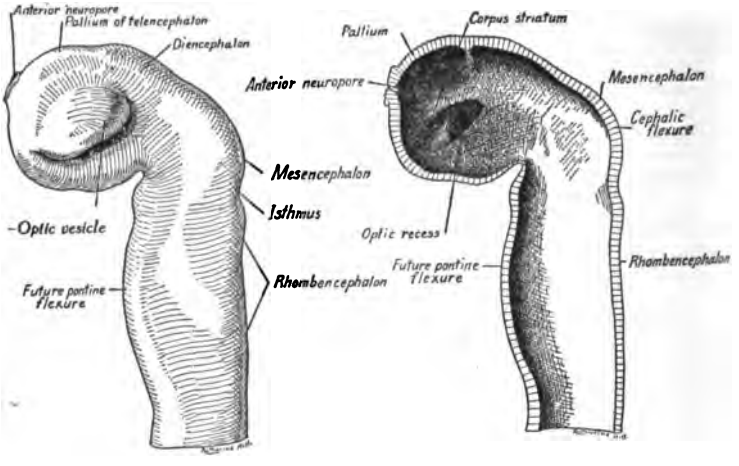

Fig. 46.—An enlarged model of the brain of a human embryo 3.2 mm. long (about two weeks old). The outer surface is shown at the left, and on the right the inner surface after division of the model in the median plane. The *Anterior neuropore* marks a point where the neural tube is still open to the surface of the body. The *Pallium* is the region from which the cerebral cortex will develop. The *Optic recess* marks the portion of the lateral wall of the *Diencephalon* from which the hollow *Optic vesicle* has evaginated. (After His, from Prentiss' Embryology.)

official names. The B. N. A. terms or their English equivalents are used in this work, save in a few cases which are specifically mentioned. The terminology of the brain is based upon the embryological researches of Professor His, and can best be outlined by reviewing the form of the human brain at a few selected stages of development.

The B. N. A. terminology was developed with exclusive reference to the human body. The names of many parts of the bodies of other animals than man and of microscopic structures in general are not included. The names of this list are all used and defined in W. Krause's Handbuch der

Anatomie des Menschen, Leipzig, 1905, and in most of the recent American and English text-books of anatomy. At the end of Krause's book is a very complete list of synonyms, including most of the anatomical terms in use and their B. N. A. equivalents. The B. N. A. tables of names with their English equivalents are given in Barker's Anatomical Terminology (1907), and Eycleshymer's Anatomical Names (1917) includes a full reprint of these tables with a translation of the accompanying annotations, followed by biographical sketches of anatomists prepared by Roy L. Moodie and by a full index of synonyms.

Following the example of many other recent anatomists, we shall in this work replace the B. N. A. term "anterior" (on the front or belly side) by the word "ventral," and the B. N. A. term "posterior" (on the back side) by the word "dorsal." The head end of the body will be referred to as the "anterior" or "cephalic" end; the other end of the body as the "posterior" or "caudal" end. The terms "upper" or "higher" and "lower" will refer to the relations in the erect human body. In the nomenclature of the medulla oblongata (see p. 130) and of the thalamus (p. 182) our usage departs slightly from that of the B. N. A. Regarding the naming of fiber tracts see page 138.

Figure 46 illustrates the form of the brain in a very early human embryo. Its tubular form is very evident, and in the brain the diameter of the tube is but little greater than that of the spinal cord. The walls are thin and the cavity wide. In a slightly older embryo the form is shown in Fig. 47, and Fig. 48 illustrates diagrammatically the median section of an embryo of about the same age as that shown in Fig. 47, upon which the regions as defined by the B. N. A. are indicated.

The brain as a whole is the encephalon, and its chief divisions are indicated by prefixes having a topographic significance applied to this word. In Fig. 48 the ventral part of the neural tube is shaded to indicate the region in which the motor centers of the adult brain are found. The unshaded part of the figure indicates the region devoted to the primary sensory centers and the correlation centers related to them. The sensory and motor regions are separated in early embryologic stages by a longitudinal limiting sulcus (the sulcus limitans). Comparison with the figures of later stages which follow shows that the suprasegmental structures are developed wholly from the sensory region. Figures 49 and 50 illustrate later stages of development and Fig. 51 the adult brain in median section. The external form of the adult brain is illustrated also in Figs. 52, 53, 54.

The table on p. 129 summarizes the relations of the subdivisions of the brain (the ventricles of some of them being added in parentheses), to which a few comments are here added.

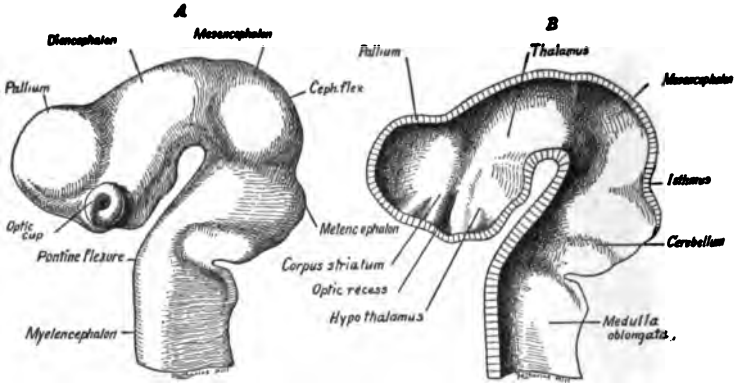

Fig. 47.—Reconstruction of the brain of a 6.9 mm. human embryo (about four weeks old): *A*, Lateral view; *B*, in median sagittal section; *Ceph.flex.*, cephalic flexure. (After His, from Prentiss' Embryology.)

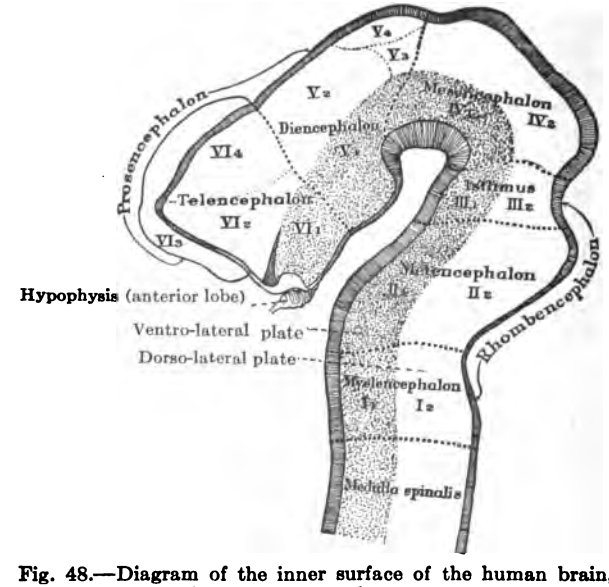

Fig. 48.—Diagram of the inner surface of the human brain, based on a specimen of about the same age as shown in Fig. 47. The shaded area is the ventro-lateral plate of the neural tube, giving rise to the motor centers. Its upper boundary is marked by a groove on the ventricular surface, the sulcus limitans, which separates the ventro-lateral plate from a dorso-lateral plate (unshaded), which gives rise to the sensory centers and chief correlation centers. (After His, from Morris' Anatomy.)

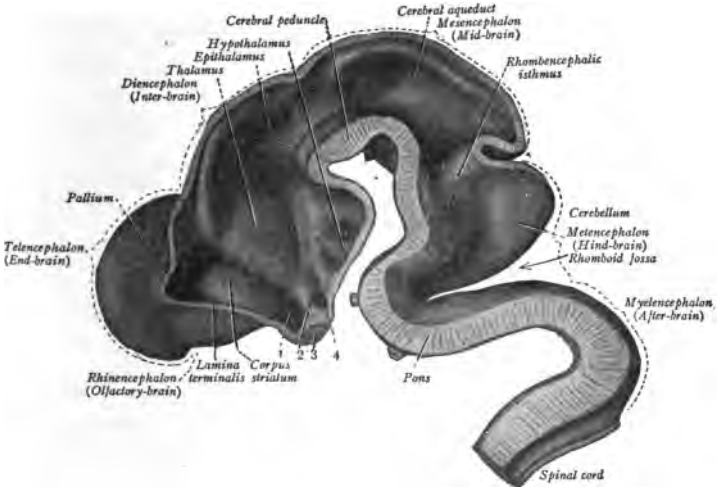

Fig. 49.—Vertical median section of a model of the brain of a human embryo 13.6 mm. long: 1, Optic recess, marking the attachment of the optic vesicle; 2, ridge formed by the optic chiasma; 3, optic chiasma; 4, infundibular recess. The limiting sulcus is visible in the model, though not named, running upward from the optic recess between the thalamus and the hypothalamus. (After His, from Sobotta's Atlas of Anatomy.)

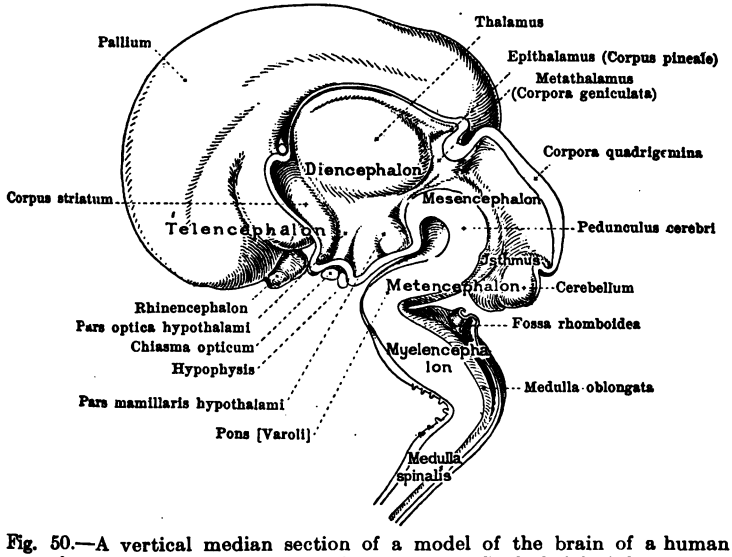

Fig. 50.—A vertical median section of a model of the brain of a human fetus in the third month. (After His, from Spalteholz's Atlas.)

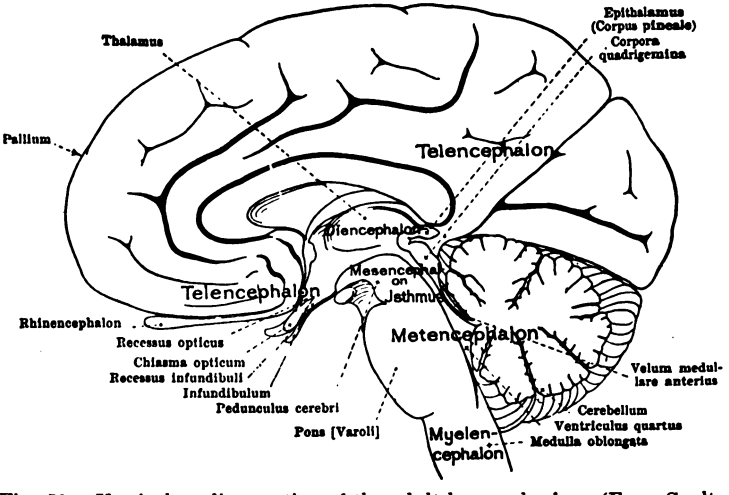

Fig. 51.—Vertical median section of the adult human brain. (From Spalteholz's Atlas.)

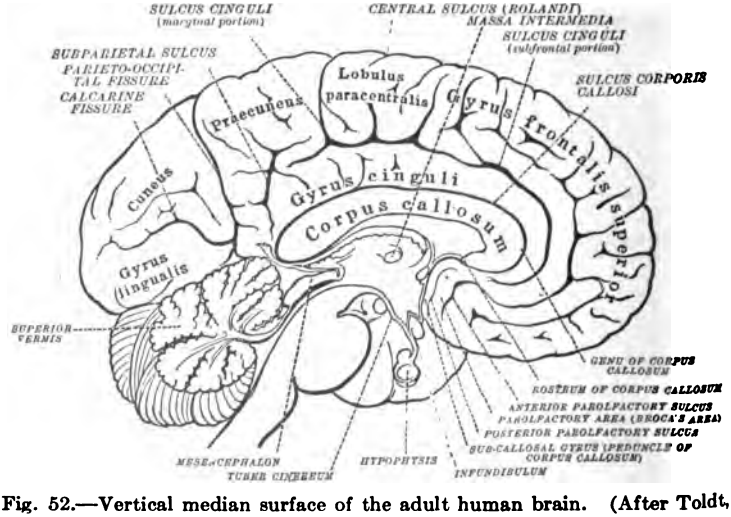

Fig. 52.—Vertical median surface of the adult human brain. (After Toldt, from Morris' Anatomy.)

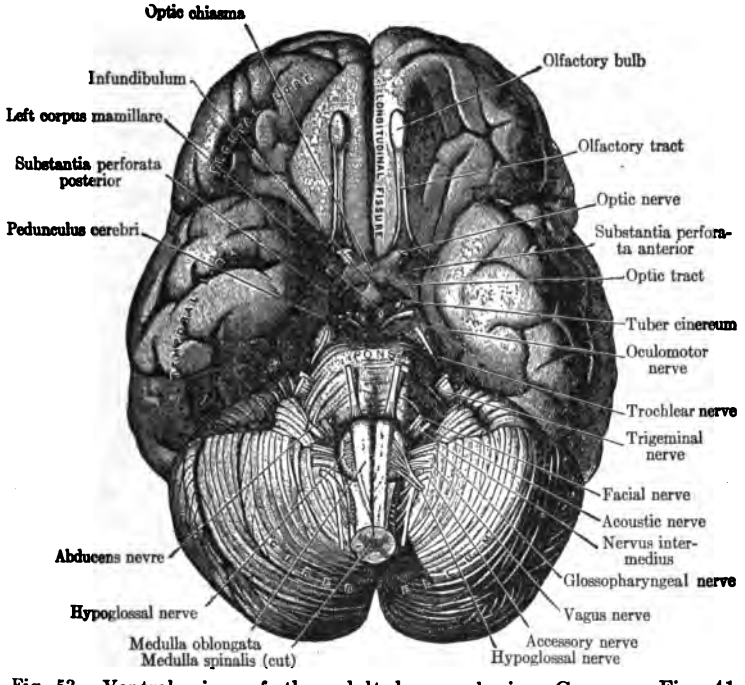

Fig. 53.—Ventral view of the adult human brain. Compare Fig. 41. (From Cunningham's Anatomy.)

Rhombencephalon, rhombic brain (fourth ventricle).
  Myelencephalon, medulla oblongata.
  Metencephalon.
    Cerebellum.
    Pons.
Isthmus rhombencephali.
Cerebrum.
  Mesencephalon, midbrain or corpora quadrigemina and cerebral peduncles (aqueduct of Sylvius).
  Prosencephalon, forebrain.
    Diencephalon, betweenbrain (third ventricle).
      Hypothalamus.
      Thalamus.
      Metathalamus.
      Epithalamus.
    Telencephalon, endbrain.
      Pars optica hypothalami.
      Hemisphæria, cerebral hemispheres (lateral ventricles).

The isthmus is a sharp constriction which separates the brain into two major divisions, the rhombencephalon behind and the cerebrum in the front. In the B. N. A. table the isthmus is regarded as a transvere segment or ring; it might better be regarded simply as a plane of separation between the rhombencephalon and cerebrum. In the table the medulla oblongata is regarded as synonymous with myelencephalon, that is, the region between the pons and the spinal cord. The older usage, which is still widely current, regards the medulla

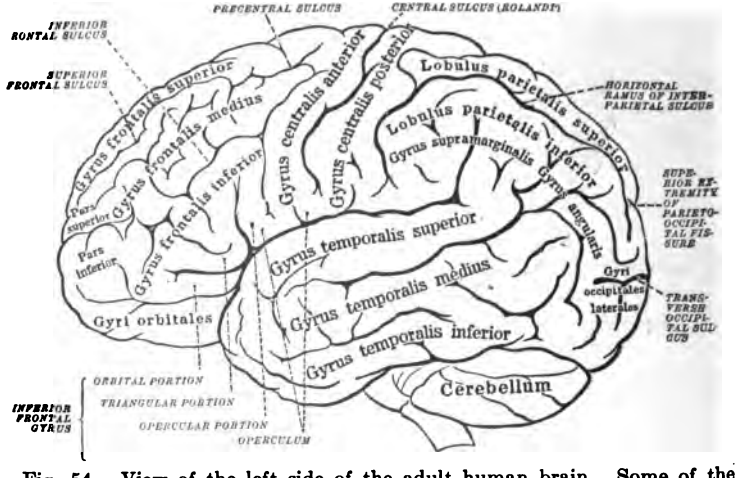

Fig. 54.—View of the left side of the adult human brain. Some of the principal sulci and gyri are named. The lateral cerebral fissure (sylvian fissure) is not named; it lies immediately above the gyrus temporalis superior. (After Toldt, from Morris' Anatomy.)

oblongata as including everything between the isthmus and the spinal cord except the cerebellum dorsally and the fibers and nuclei of the pons and middle peduncle of the cerebellum ventrally. This is the old or segmental part of the rhombencephalon, and the cerebellum and pons fibers related to it are added to this primitive medulla oblongata. The older usage is preferable to the B. N. A. division and will be adopted here, for the medulla oblongata as here defined is a structural and functional unit, whose form is not modified in those animals which almost totally lack the cerebellum and its middle

peduncle. As indicated on page 158, the medulla oblongata may be divided on functional and morphological grounds into an upper or facial part and a lower or visceral part (the myelencephalon of the B. N. A.).

The midbrain (mesencephalon) is the least modified part of the embryonic neural tube in the adult brain. The part above the ventricle (corpora quadrigemina) contains important correlation centers for optic and auditory reflexes (p. 175); the part below the ventricle (cerebral peduncle) contains primary motor centers for movement of the eyeball and motor coördination centers.

The betweenbrain (diencephalon) has three principal divisions: (1) below is the hypothalamus; (2) above is the epithalamus; (3) between these is the thalamus which includes the thalamus and metathalamus of the table (see p. 182). The hypothalamus and epithalamus are highly developed in the lowest vertebrates and are related to the olfactory apparatus; in these brains the thalamus proper is very small, this part increasing in size in the higher animals parallel with the evolution of the cerebral cortex. The thalamus proper is really a sort of vestibule to the cerebral cortex; all nervous impulses which reach the cortex, except those from the olfactory organs, enter it through the thalamus. The endbrain (telencephalon) includes the cerebral hemispheres and a very small part of the primitive unmodified neural tube to which the hemispheres are attached, this being the pars optica hypothalami of the table or, better, the telencephalon medium.

If now we compare this subdivision of the human brain with our rough functional analysis of the fish brain (p. 120), we notice that the "ear brain" (acoustico-lateral area), "skin brain" or "face brain" (general cutaneous area), and "visceral brain" (visceral area) are all contained in the rhombencephalon, whose segmental or stem portion is made up of these centers and the corresponding motor centers. The same relations hold in the human brain, and in both cases the cerebellum (and in man the pons in the narrower sense in which I use that term) is added as a suprasegmental part. In both cases the "eye brain" includes the retina of the eye, the optic nerve, and a part of the roof of the midbrain. In the fish a very small part of the thalamus (not indicated on Figs.

43 and 44) also receives fibers from the optic nerve. In man this optic part of the thalamus is greatly enlarged, forming so large a part of that structure in fact that the thalamus as a whole is often called the optic thalamus. It should be remembered, however, that even in man the optic centers comprise only a part of the thalamus. The "nose brain" of the fish comprises most of the cerebral hemispheres, and also of the epithalamus and hypothalamus. In man these parts remain essentially unchanged, but there have been added the large corpus striatum and the enormous cerebral cortex, the latter forming the suprasegmental apparatus of the telencephalon, and greatly modifying the form relations of all adjacent parts.

The details of the development of the brain lie outside the scope of this work, as also do the anthropological questions growing out of the statistical study of brain weights[1] and measurements. These and many other topics of fundamental importance are presented in a very interesting way in Donaldson's book on The Growth of the Brain.

The Meninges.—The central nervous system is enveloped by three membranes, from without inward, the dura mater, arachnoid, and pia mater. These membranes in the aggregate are called meninges.

The *dura mater* of the brain is a dense fibrous membrane closely adherent to the skull, for which it serves also as the inner nourishing membrane (periosteum). These two functions are performed by separate parts of the membrane in the spinal region, where the bones of the spinal column are provided with a separate inner periosteal covering and the spinal cord is enveloped by a distinct cylindrical membranous dura mater, the two being separated by a wide epidural space.

A fold of dura mater extends downward into the longitudinal fissure between the two cerebral hemispheres (falx cerebri), and a similar fold extends transversely in the great fissure between the cerebrum and the cerebellum (tentorium cerebelli).

The *arachnoid* is a very delicate membrane adherent to the dura with a far less compact layer adherent less closely to the pia. There are numerous subarachnoid spaces filled with fluid between the outer arachnoid and the pia.

The *pia mater* is a delicate and very vascular membrane which follows the contour of the brain very closely and from which the greater part of the internal blood-vessels of the brain are derived.

The Choroid Plexuses.—In the development of the brain from the embryonic neural tube there are four parts of the brain walls which remain

[1] The weight of the brain is exceedingly variable, even in a homogeneous population. The average weight of the normal adult European male brain is commonly stated to be 1360 grams (48 oz.), and that of the female 1250 grams (44 oz.).

thin and non-nervous. Each of these regions is known as an epithelial plate (*lamina epithelialis*). One of these is seen as the "Roof plate" of Fig. 70, p. 167. The pia mater which covers these epithelial plates is called the *tela chorioidea*. A portion of each of the four epithelial plates is greatly enlarged and thrust into the underlying brain ventricle in the form of a crumpled fold. The outer surface of these folded epithelial membranes is closely covered by highly vascular pia mater, and this portion of the pia is called a choroid plexus (*plexus chorioideus*). We have, accordingly, a choroid plexus in the lateral ventricle of each cerebral hemisphere (Fig. 107, p. 248), a choroid plexus of the third ventricle (Fig. 79, p. 181), and a choroid plexus of the fourth ventricle.

The *cerebrospinal fluid* is a clear liquid differing in chemical composition from the lymph; it fills the ventricles of the brain, the central canal of the spinal cord, and the subarachnoid spaces. Some of the subarachnoid spaces are greatly enlarged to form the so-called cisterns, as the cisterna cerebello-medullaris (or magna) between the medulla oblongata and the cerebellum.

The functions of the cerebrospinal fluid are not clearly understood. It seems to be derived from both the choroid plexuses and the general brain tissue. There are no definite lymph vessels within the brain or meninges and this fluid may serve, like the lymph in other parts of the body, to carry nutrient and waste materials concerned in the metabolism of the brain tissue (see Halliburton, 1916, Weed, 1917, and the papers there cited). The choroid plexuses have been shown to produce oxidases (Pighini, 1912), which are present in the cerebrospinal fluid also, and it has been suggested that this aids in maintaining metabolism in brain tissue.

Summary.—In all vertebrates the central nervous system is fundamentally a hollow dorsal tube in which the primary segmentation is subordinated to the development of important longitudinal correlation tracts and centers. This tube is enlarged at the front end to form the brain. The vertebrate brain may be divided on physiological grounds into great divisions, first the brain stem, or primary segmental apparatus; and second the cerebellum and cerebral cortex, or suprasegmental apparatus. The brain stem and cerebellum are devoted chiefly to reflex and instinctive activities and constitute the "old brain" of Edinger. The cerebral cortex is devoted to the higher associations and individually acquired activities and is called the "new brain" by Edinger. No nervous impulses can enter the cortex without first passing through the reflex centers of the brain stem.

In fishes the form of the brain is shaped almost wholly by the development of the reflex centers, and here these mechanisms can best be studied, each of the more obvious parts of the brain being dominated by a single system of sensori-motor

reflex circuits. The same pattern is preserved in the human brain, but much distorted by the addition of the centers of higher correlation.

The terminology of the brain now in most common use is based on its embryological development, which is briefly reviewed.

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CHAPTER VIII

THE SPINAL CORD AND ITS NERVES

THE spinal cord (*medulla spinalis*) is the least modified part of the embryonic neural tube, and the spinal nerves constitute the only part of the nervous system in which the primitive seg-

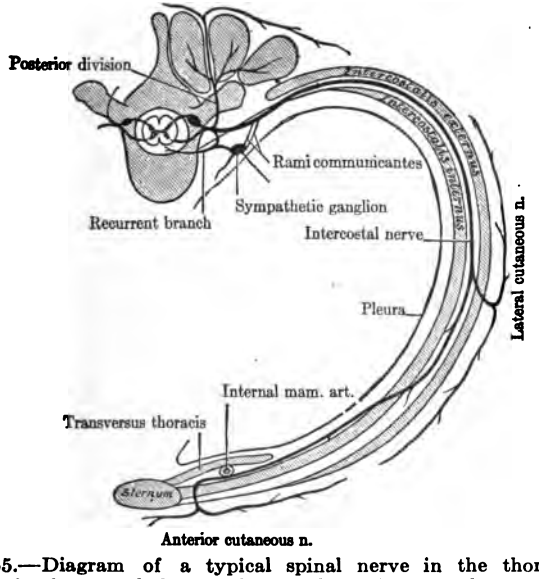

Fig. 55.—Diagram of a typical spinal nerve in the thoracic region. The spinal column and the muscles are shown in gray, the nerves and their ganglia in black. (From Gray's Anatomy.)

mental pattern is clearly preserved in the adult body (see p. 121). The spinal nerves are connected with the spinal cord in serial order, a pair of nerves for each vertebra of the spinal column (see Fig. 41, p. 115).

Each spinal nerve distributes efferent (motor) fibers to the muscles and afferent (sensory) fibers to the skin and deep tissues of its appropriate segment of the body, and through its connections with the sympathetic nervous system it may effect various visceral connections (Figs. 55 and 56). The efferent fibers leave the cord through the ventral roots of the spinal nerves, these fibers arising from cells within the gray matter of the cord, and the afferent fibers enter through the dorsal roots,

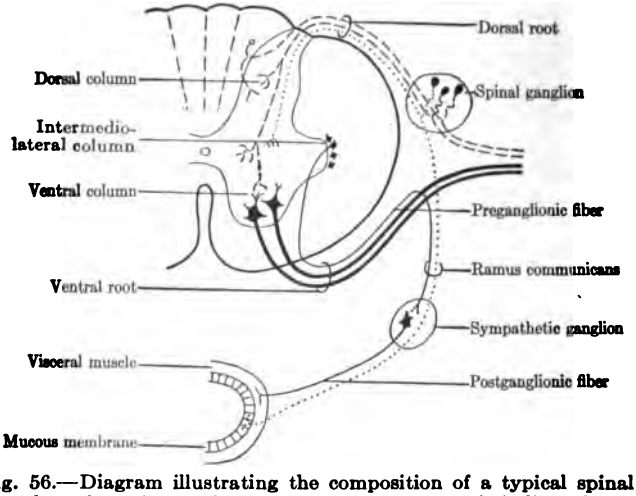

Fig. 56.—Diagram illustrating the composition of a typical spinal nerve in the thoracic region. The somatic sensory system is indicated by broken lines, the visceral sensory by dotted lines, the somatic efferent by heavy continuous lines, the visceral efferent by lighter continuous lines. (Compare Figs. 1 and 55.)

these fibers arising from cell bodies of the spinal ganglia (see Fig. 1, p. 26, and Figs. 55, 56). The fibers of the spinal nerves are best classified in accordance with the same physiological criteria as their end-organs (see pp. 84–99, and compare the cranial nerves, pp. 155–165) into somatic afferent (or sensory), visceral afferent (or sensory), somatic efferent (or motor), and visceral efferent (or motor) systems (Fig. 56).

In the spinal cord the originally wide cavity of the embryonic neural tube (see p. 125) is reduced to a slender central canal

and the walls of the tube are thickened. The nerve-cells retain their primary position bordering the central canal, thus forming a mass of central gray matter which is roughly H-shaped in cross-section. This gray matter on each side is accumulated in the form of two massive longitudinal ridges, a dorsal column (*columna dorsalis*, or posterior horn), whose neurons receive terminals of the sensory fibers of the dorsal roots, and a ventral column (*columna ventralis*, or anterior horn) whose neurons give rise to the fibers of the ventral roots.

The white matter of the spinal cord is superficial to the gray and is made up of sensory and motor root fibers of spinal nerves, ascending and descending correlation fibers putting different parts of the cord into functional connection, and longer ascending and descending tracts by which the spinal nerve-centers are connected with the higher association centers of the brain. In general, the shorter fibers lie near to the central gray and the longer tracts more superficially.

The white matter which borders the gray in the spinal cord is more or less mingled with nerve-cells and fine unmyelinated endings, and thus shows under low powers of the microscope a reticulated appearance. This is the reticular formation (processus reticularis) of the cord (see pp. 69, 172, and Fig. 58). Immediately surrounding the reticular formation and partly embedded within it are myelinated fibers belonging to neurons intercalated between the sensory and the motor roots, which run for relatively short distances in an ascending or descending direction for the purpose of putting all levels of the cord into functional connection in the performance of the more complex spinal reflexes. These fibers form the deepest layer of the white matter and are termed the *fasciculi proprii* (dorsalis, lateralis, and ventralis, see Fig. 59). These fascicles are also called ground bundles and fundamental columns.

In the narrow space between the ventral fissure and the central canal (see Fig. 58) there is a bundle of nerve-fibers which cross from one side of the spinal cord to the other. This is the ventral commissure. A similar but smaller dorsal commissure crosses immediately above the central canal.

There is considerable confusion in the terminology in use in the further analysis of the spinal white matter, and the usage which follows differs

in some respects from most of the classical descriptions, no two of which agree among themselves. We shall limit the application of the term *funiculus* to the three major divisions of the white matter of each half of the spinal cord, viz., the dorsal funiculus bounded by the dorsal fissure and the dorsal root, the lateral funiculus lying between the dorsal and ventral roots, and the ventral funiculus between the ventral root and the ventral fissure (Fig. 57).

Each funiculus may be divided in a purely topographic sense into *fasciculi*, or collections of nerve-fibers which occupy the same general region in the cross-section of the cord, such as the fasciculus gracilis of Goll and the fasciculus cuneatus of Burdach (which together make up the greater part of the funiculus dorsalis, see Figs. 57 and 59), and the superficial ventro-lateral fasciculus of Gowers (including among other tracts the spino-tectal tract and the ventral spino-cerebellar tract of Fig. 59). These fasciculi are usually mixed bundles containing tracts of diverse functional types.

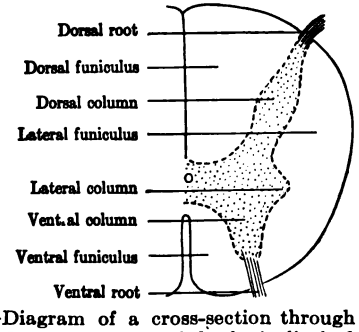

Fig. 57.—Diagram of a cross-section through one-half of the spinal cord to illustrate the arrangement of the funiculi of white matter and the columns of gray matter.

The true physiological units of the spinal white matter are the *tracts*, *i. e.*, collections of nerve-fibers of similar functional type and connections. Some of these tracts are often termed fasciculi; and, like the other tracts of the central nervous system, they are, in general, named in accordance with the terminal relations of their fibers, the name of the location of their cells of origin preceding that of their place of discharge in a hyphenated compound word. Thus, the tractus cortico-spinalis arises from cells of the cerebral cortex (p. 151), and terminates in the spinal cord, and the tractus spino-cerebellaris arises in the spinal cord and terminates in the cerebellum (p. 140). But, as already stated, there is no uniformity in the nomenclature of these tracts and no two authorities agree exactly in the terminology adopted. Moreover, few of the tracts have clearly defined anatomical limits, in most cases the fibers of different systems being more or less mingled.

The appearance of a cross-section through the spinal cord in the lower cervical (neck) region, after staining so as to reveal

the arrangement of both the nerve-cells and the nerve-fibers, is seen in Fig. 58. Figure 59 illustrates diagrammatically the arrangement of the chief fiber tracts in the same region.

The spinal cord has two main groups of functions, first, as a system of reflex centers for all of the activities of the trunk and limbs; second, as a path of conduction between these centers and the higher correlation centers of the brain. The former

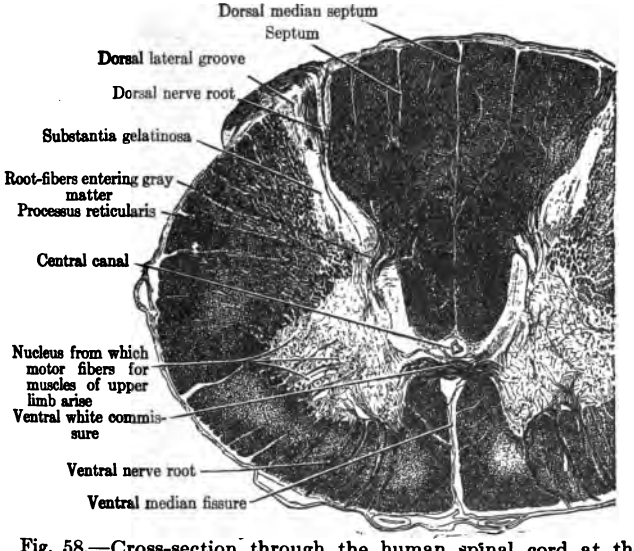

Fig. 58.—Cross-section through the human spinal cord at the level of the fifth cervical nerve, stained by the method of Weigert-Pal, which colors the white matter dark and leaves the gray matter uncolored. (From Cunningham's Anatomy.)

group is the more primitive, and there is evidence that in the course of vertebrate evolution the higher centers, especially the cerebral hemispheres, exert an increasingly greater functional control over these reflex centers (see p. 314). The long conduction paths between the spinal cord and the cerebral hemispheres are, accordingly, much larger in man than in lower vertebrates. It is impossible in the space at our disposal to summarize even the most important of the internal connec-

tions of the spinal nerves; we can only select a few typical illustrative examples.

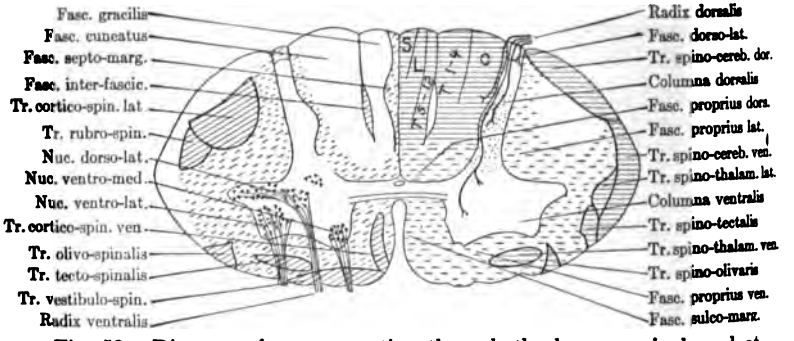

Fig. 59.—Diagram of a cross-section through the human spinal cord at the level of the fifth cervical nerve, to illustrate the arrangement of the fiber tracts in the white matter and of the nerve-cells in the gray matter of the ventral column. On the right side the area occupied by the dorsal gray column (posterior horn) is stippled; on the left side some of the groups of cells of the ventral gray column (anterior horn) are indicated. In the white matter the outlines of some of the more important tracts are schematically indicated, ascending fibers on the right side and descending fibers on the left. The same area of white matter is in some cases shaded on both sides of the figure. This indicates that ascending and descending fibers are mingled in these regions. A list of the tracts here illustrated follows. The names here employed in some cases differ from those of the official German Anatomical Society list (see p. 124), the B. N. A. terms here being italicized.

Ascending Tracts

Fasciculus gracilis (column of Goll) and *fasciculus cuneatus* (column of Burdach). These are mixed bundles which in the aggregate make up the greater part of the dorsal funiculus (old term, posterior columns). They are made up chiefly of the ascending branches of dorsal root fibers (see Fig. 61), those in the gracilis from the sacral, lumbar, and lower thoracic nerves (*S*, *L*, *T*5–12), and those in the cuneatus from the upper thoracic and cervical nerves (*T*1–4, *C*), as indicated in the figure. These fasciculi terminate respectively in the nuclei of the fasciculus gracilis (clava) and cuneatus (tuberculum cuneatum) at the lower end of the medulla oblongata (cf. Fig. 83), and conduct chiefly impulses of the proprioceptive reflexes and those concerned with sensations of posture, spatial discrimination, and the coördination of movements of precision (see pp. 149, 192).

Fasciculus dorso-lateralis (tract of Lissauer, Lissauer's zone), made up chiefly of unmyelinated fibers from the dorsal roots, together with myelinated correlation fibers of the fasciculus proprius system.

Tractus spino-cerebellaris dorsalis (*fasciculus cerebello-spinalis*, direct

cerebellar tract, Flechsig's tract). These fibers arise from the neurons of the *nucleus dorsalis* (Clarke's column of gray matter between the dorsal and ventral gray columns in the thoracic region, also called Stilling's nucleus) of the same side and enter the cerebellum by way of its inferior peduncle (*corpus restiforme*).

Tractus spino-cerebellaris ventralis (part of Gowers' tract, or the *fasciculus antero-lateralis superficialis* of the *B. N. A.*). These fibers also arise from the nucleus dorsalis of the same side in monkeys (A. N. Bruce) in the lower levels of the spinal cord and enter the cerebellum by way of its superior peduncle (*brachium conjunctivum*). In man they are said to arise from the corresponding region of the cord (though the nucleus dorsalis is not here recognizable), and many of them are believed to decussate in the ventral commissure.

The spinal lemniscus. Under this name are included several tracts to the midbrain and thalamus. These fibers arise from neurons of the dorsal gray column, cross in the ventral commissure, and ascend in the lateral and ventral funiculi of the opposite side, partly superficially mingled with those of the ventral spino-cerebellar tract and partly deeper in the fasciculus proprius. This system of fibers includes a tractus spino-tectalis to the roof (tectum) of the midbrain and a tractus spino-thalamicus to the ventral and lateral nuclei of the thalamus. The deeper fibers of the latter tract are arranged in two groups, the tractus spino-thalamicus lateralis for sensory impulses of temperature and pain, and the tractus spino-thalamicus ventralis for sensory impulses of touch and pressure (see pp. 149, 189).

Tractus spino-olivaris, fibers arising from the entire length of the spinal cord and terminating in the inferior olive (Goldstein).

Descending Tracts

Tractus cortico-spinalis (*fasciculus cerebro-spinalis*, pyramidal tract). This system of fibers conducts voluntary motor impulses from the precentral gyrus of the cerebral cortex to the motor centers of the spinal cord. It divides at the upper end of the spinal cord into two tracts, the larger division immediately crossing through the decussation of the pyramids to the opposite side of the spinal cord, where it becomes the tractus cortico-spinalis lateralis (*fasciculus cerebro-spinalis lateralis*, lateral or crossed pyramidal tract). A smaller number of these fibers pass downward into the spinal cord from the medulla oblongata without decussation to form the tractus cortico-spinalis ventralis (*fasciculus cerebro-spinalis anterior*, direct pyramidal tract, column of Türck). These fibers cross in the ventral commissure a few at a time throughout the upper levels of the cord, and finally terminate in the cervical and upper thoracic regions in relation with the motor neurons of the opposite side. Both parts of the pyramidal tract, therefore, decussate before their fibers terminate (see p. 319).

Tractus rubro-spinalis (tract of Monakow), from the nucleus ruber of the midbrain to the spinal cord, for thalamic and cerebellar reflexes. They cross in the ventral tegmental decussation (Fig. 75, p. 176).

Tractus olivo-spinalis (Helwig's bundle, tractus triangularis), fibers descending from the inferior olive of the medulla oblongata to the lower cervical or upper thoracic segments of the spinal cord.

Tractus tecto-spinalis (predorsal bundle, tract of Löwenthal), from the roof (tectum) of the midbrain to the spinal cord, chiefly for optic reflexes. Part of these fibers cross in the dorsal tegmental decussation, or fountain decussation of Meynert (Fig. 75, p. 176).

Tractus vestibulo-spinalis, from the primary centers of the vestibular nerve in the medulla oblongata to the spinal cord, for equilibratory reflexes.

The two tracts last mentioned, together with several others, compose the fasciculus marginalis ventralis.

The Fasciculus Proprius

The fasciculus proprius system of fibers (also called ground bundles, basis bundles, and fundamental bundles) comprises chiefly short ascending and descending fibers arising from neurons of the spinal gray matter, for intrinsic spinal reflexes. In general, these fibers border the gray pattern, but in the dorsal funiculus some are aggregated in the tractus septo-marginalis and the fasciculus interfascicularis (comma tract, tract of Schultze), these two tracts also containing descending branches of the dorsal root fibers. Some fibers of the fasciculus proprius ventralis lie adjacent to the ventral fissure and are termed the fasciculus sulcomarginalis, these fibers forming the direct continuation into the cord of the fasciculus longitudinalis medialis (posterior longitudinal bundle) of the brain (see pp. 204, 237).

The sensory nerves which enter the spinal cord come either from the deep tissues or from the skin, and both of these types of nerves carry fibers of very diverse functional sorts belonging to the somatic sensory group, in addition to visceral fibers which will not be considered here. It will be recalled (see pp. 82, 84) that the general somatic sensory group includes: (1) proprioceptive systems, concerned with motor coördination and the orientation of the body and its members in space (muscle sense, tendon sense, etc.), and (2) exteroceptive systems, concerned with the relations of the body to its environment (touch, temperature, and pain sensibility). The first of these systems is served chiefly by the deep nerves, and the second chiefly by the cutaneous nerves, though this is not rigidly true. In particular it should be noted that, even though the skin be completely anesthetic, the nerves of deep sensibility can still respond not only to their proprioceptive functions, but also to the ordinary clinical tests for the exteroceptive qualities of touch, temperature, and pain, though with a higher threshold than in the case of the cutaneous end-organs of these senses.

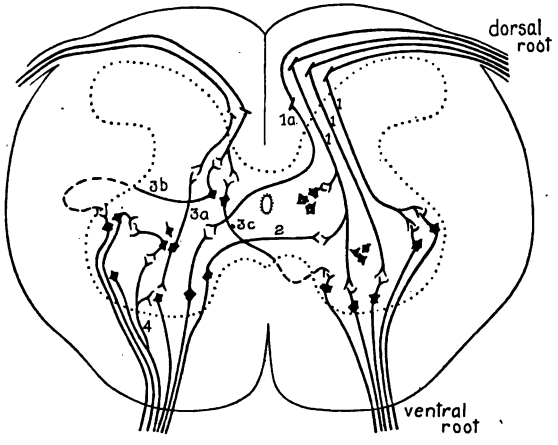

Fig. 60.—Diagram of some of the types of connection between the sensory fibers of the dorsal root and the motor fibers of the ventral root in the spinal cord of the rabbit (chiefly after the researches of Philippson). The visceral connections are not included.

1. Collateral branches of the dorsal root fibers effect synaptic relations directly with dendrites of ventral column cells of the same or the opposite side.

2. Dendrites of ventral column cells may cross to the opposite side and here receive terminals of dorsal root fibers.

3. A correlation neuron may be intercalated between the two peripheral neurons in either of the first two cases. These neurons may have short axons for reflexes within a single segment (3*a*) or their axons may pass out into the white matter (fasciculus proprius) and extend for longer or shorter distances in either the ascending or the descending direction (or after branching in both directions) for connections with more remote motor centers of the same or the opposite side (3*b*, 3*c*).

4. The root fibers arising from the cells of the ventral column themselves may give off collateral branches which return to the gray matter and there arborize about other cells of the ventral column belonging to different functional groups or about correlation cells, thus facilitating the coördinated contraction of several distinct muscles in the performance of some complex reaction.

The neurons of the dorsal column apparently do not play an important rôle as intercalary elements in the simpler spinal reflexes. The axons of these cells are for the most part directed upward, after decussating in the ventral commissure, and are chiefly concerned with the transmission of nervous impulses from the spinal cord to the higher correlation centers of the brain.

Upon entering the spinal cord all of these functional types of fibers effect two sorts of connections: (1) for intrinsic spinal reflexes, and (2) for the transmission of their impulses upward to the higher centers of the brain. We shall first take up the intrinsic connections.

The simplest of these intrinsic connections is the direct motor reflex illustrated by Fig. 1 (p. 26), but there are many more complex forms of the connection between the dorsal and

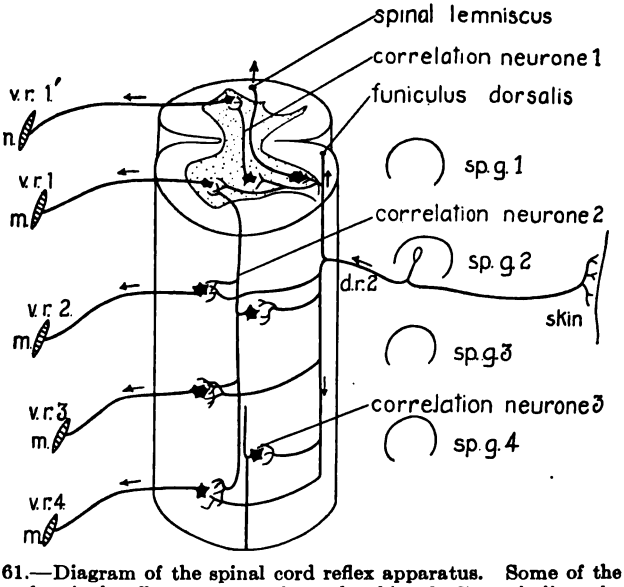

Fig. 61.—Diagram of the spinal cord reflex apparatus. Some of the connections of a single afferent neuron from the skin (*d.r.*2) are indicated: *d.r.*2, dorsal root from second spinal ganglion; *m*, muscles; *sp.g.*1 to *sp.g.*4, spinal ganglia; *v.r.*1′ to *v.r.*4, ventral roots.

ventral roots, some of which are indicated in Figs. 60 and 61. In general, there is at least one neuron of the gray matter of the spinal cord interpolated between the dorsal and the ventral root neurons, and usually there is a complex chain of such neurons. As may be observed in Fig. 61, the dorsal root fiber immediately upon entering the spinal cord divides into ascending and descending branches, and secondary branchlets are

given off in large numbers from each of these, so that a single peripheral sensory neuron may discharge its nervous impulses into very many central neurons scattered throughout the entire length of the spinal cord. When to these numerous endings we add the countless ramifications of the correlation neurons, it is evident that even in the spinal cord, which is the simplest part of the central nervous system, there are reflex mechanisms of great complexity. Some of these have been analyzed. Sherrington, in his Integrative Action of the Nervous System, has presented a very clear analysis of the scratch reflex of the dog and the neural mechanisms involved. The mechanism of the locomotor reflexes has been studied physiologically and histologically by Steiner, Philippson, Polimanti, Herrick and Coghill, and very many others.

In animals below man the spinal cord reflexes can be studied in the spinal animal (p. 68), in which the cord has been separated from the brain by high transverse section. In man, however, an injury of this type results in temporary loss of nearly all reflexes below the level of the lesion (spinal shock), and it was formerly believed that there is possibility of very little subsequent improvement. But recently (Riddoch, 1917) under more skilful treatment such patients show recovery of considerable reflex activity. After a period of spinal shock lasting from one to three weeks, there is gradual return of reflex motility, especially of the flexor systems of muscles and in general of reflexes originated by stimuli which in the intact individual have a strong affective quality.

Our most precise knowledge of the arrangement of the afferent and efferent myelinated fibers in the spinal roots has been gained by the application of Marchi's method (p. 50) to the study of degenerations following accidental and experimental injuries. Nerve-fibers which have been cut off from their cells of origin degenerate within about two weeks after the injury. It is, therefore, possible by the microscopic study of a divided nerve with Marchi's method (which stains only the degenerating myelinated fibers) to determine on which side of the injury are the cells of origin from which these fibers arise.

Figure 62 illustrates the effects of section of the spinal roots made at four different places. In the first case section of the mixed trunk peripherally of the union of the dorsal and ventral roots is followed by degeneration of all of the myelinated fibers of the nerve-trunk, showing that the cell bodies of all of these

fibers lie centrally of the injury. In the second case, section of the ventral root close to the spinal cord is followed by degeneration of all the fibers of this root without disturbance of those of the dorsal root, showing that the ventral root fibers arise as axons of cells within the spinal cord. In the third case section

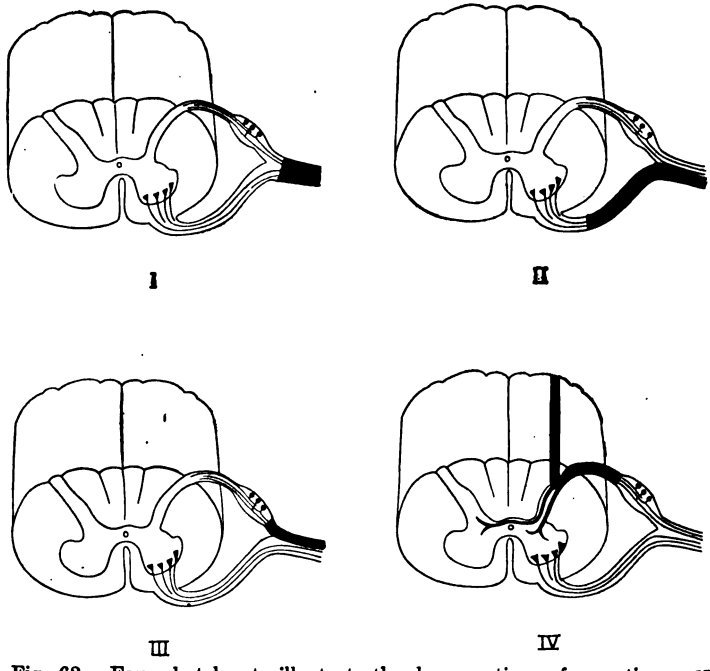

Fig. 62.—Four sketches to illustrate the degenerations of somatic sensory and motor fibers which follow section of spinal nerve-roots in different places. Fibers separated from their cells of origin will degenerate, as shown in black (see the text, p. 145).

of the dorsal root fibers peripherally of the ganglion and before their union with those of the ventral root results in the degeneration of all of the fibers of the mixed nerve which arise in the spinal ganglion (sensory fibers), without loss of any motor fibers from the ventral root. In the fourth case section of the

dorsal root on the central side of the ganglion is followed by degeneration of all myelinated fibers of the central stump of this root, but not of the peripheral part of the root or the spinal ganglion. This shows that the cells of origin of these fibers lie in the spinal ganglion and not, like those of the ventral root, within the spinal cord. The peripheral processes of these ganglion cells, therefore, are dendrites, and the centrally directed processes which compose the dorsal roots are axons (cf. Fig. 1, p. 26, and Fig. 56, p. 136).

Another useful method for the solution of problems of this character is the study of the fine structure of the cell bodies of the neurons after such experimental lesions as those just described. Neurons whose peripheral fibers have been severed, thus cutting the cell body off from its usual avenue of functional discharge, within a few days thereafter undergo structural changes, chief of which is chromatolysis, or the solution and disappearance of the Nissl bodies (see p. 50). Thus, after cutting a ventral spinal root (Fig. 62, II), a microscopic examination of the spinal cord will show the chromatolysis effect (see Fig. 13, p. 51) in every neuron in the ventral gray column which gives rise to a fiber of this root, while all of the other neurons will remain normal.

Physiological experiments upon men and other animals where such injuries have taken place give the necessary control to confirm the proof that efferent fibers leave the spinal cord through the ventral roots and afferent fibers enter through the dorsal roots, for the loss of ventral roots results in a motor paralysis of the muscles supplied by them, while the destruction of dorsal roots results in the loss of superficial and deep sensibility in the regions innervated, with no loss of motor function save for the imperfect coördination resulting from the loss of the sensory control through the proprioceptive system (ataxia).

By the use of these and other methods, together with careful dissections, the peripheral functional connections of all of the spinal nerves have been determined, as given in Reid's chart (p. 69) and other similar tables.

The neurons of the ventral gray column are arranged in

elongated groups or nuclei, each of which is related to special systems of muscles. These nuclei are sometimes called columns and are of three types: (1) The medial groups supply the somatic muscles of the trunk. They extend throughout the length of the cord. (2) The lateral groups supply the muscles of the limbs and are limited to the cervical and lumbosacral enlargements. (3) The intermediolateral or lateral visceral group supplies preganglionic fibers to the sympathetic nervous system. It is present only in those segments which possess communicating branches between the spinal and sympathetic nerves. There are other special groups of neurons in the dorsal gray column and in the body of the gray substance, such as the substantia gelatinosa and the nucleus dorsalis of Clarke. The neurons of the dorsal column are chiefly concerned with the transmission of exteroceptive nervous impulses to the brain, those of the nucleus dorsalis of Clarke and related groups with proprioceptive impulses to the cerebellum, and the more centrally placed groups with various intrinsic reflexes of the spinal cord itself.

Turning now to the conduction paths between the spinal cord and the brain, we notice first that the reactions involved here may be performed either reflexly or consciously. In the latter case a connection with the cerebral cortex is to be expected; in the former case an infinite variety of reflex connections within the brain stem is possible.

The sensory or ascending fibers which pass between the spinal cord and the brain may be classified as follows:

I. Proprioceptive systems:
   1. To the cerebellum (unconscious).
   2. To the brain stem (unconscious).
   3. To the thalamus and cerebral cortex (sensations of posture and spatial adjustment).

II. Exteroceptive systems:
   1. To the brain stem (unconscious).
   2. To the thalamus and cerebral cortex (sensations of touch, temperature, and pain).

I. Proprioceptive Systems.—As soon as the afferent fibers of the spinal nerves have entered the spinal cord they are immediately segregated into proprioceptive and exteroceptive

groups, as suggested by the analysis above (see Figs. 63, 64, 81, and 83). The proprioceptive fibers take quite different courses, depending upon whether they are directed into the cerebellar path or into the path to the brain stem and cerebral cortex. Some terminals of this system end in the gray matter between the dorsal and ventral columns (the nucleus dorsalis of Clarke,

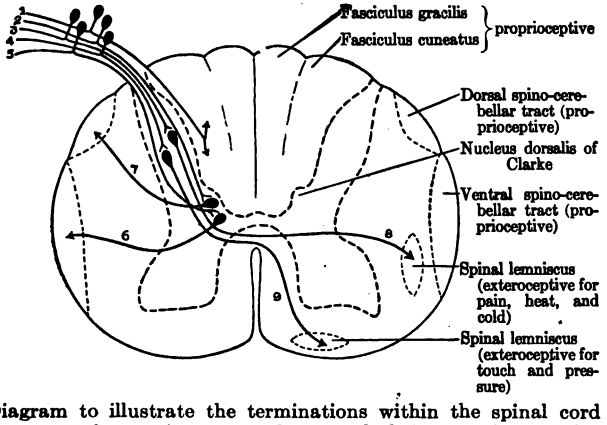

Fig. 63.—Diagram to illustrate the terminations within the spinal cord of some of the types of somatic sensory fibers and their secondary paths. The central connections of root fibers 1, 2, and 5 provide for proprioceptive responses; those of fibers 3 and 4, for exteroceptive responses. Root fiber 1 terminates in the nucleus of the fasciculus cuneatus of the same side at the upper end of the spinal cord and conveys impulses of muscular sensibility, sense of passive position and movement, and of spatial discrimination. Root fiber 2 terminates in the nucleus dorsalis of Clarke (Clarke's column) and root fiber 5 in the same nucleus or adjacent parts of the gray substance. These fibers call forth unconscious cerebellar activity underlying the coördination and reflex tone of the muscles. Root fibers 3 and 4 terminate in the dorsal gray column and convey exteroceptive impulses. Fiber 3 typifies all fibers which carry sensibility of pain, heat, and cold; fiber 4, those which carry sensibility of touch and pressure (see p. 141, Spinal lemniscus).

or Clarke's column, and adjacent regions), whose neurons send their axons into the dorsal and ventral spino-cerebellar tracts and finally into the cerebellum. The cerebellum is the great center of motor coördination, and these spino-cerebellar tracts are two only out of a larger number of paths by which afferent spinal impulses may be discharged into it (see p. 205).

The remaining proprioceptive fibers of the spinal roots are

directed upward in the dorsal funiculus, of which they form the larger part. At the point where the spinal cord passes over into the medulla oblongata they terminate, and after a synapse here the neurons of the second order carry the impulse across to the opposite side of the brain and upward toward the thalamus in a tract known as the medial lemniscus or fillet (Fig. 64). After another synapse here, a final neuron may carry the nervous impulse forward to the cerebral cortex. This medial lemniscus system is largely concerned with unconscious motor adjustments involving the muscles of the trunk and limbs. Disturbance of its functions produces motor incoördination (ataxia), but not necessarily any great loss of exteroceptive sensations. So far as its functions come into consciousness, they are recognized as sensations of position, spatial localization, and motor control.

II. **Exteroceptive Systems.**—The central course of the exteroceptive fibers of the spinal nerves is quite different from that just described. Almost immediately after entering the spinal cord these fibers terminate among the neurons of the dorsal gray column. After a synapse here the fibers of the second order cross to the opposite side of the spinal cord, and here turn and ascend in the white matter of the lateral and ventral funiculi, where they form the spinal lemniscus, or tractus spino-thalamicus. Some fibers of the spinal lemniscus ascend throughout the entire length of the spinal cord, medulla oblongata, and midbrain, to end in the thalamus. In the upper part of their course these fibers accompany those of the medial lemniscus already described.

Collateral connections are effected between the ascending fibers of the spinal lemniscus and the various motor nuclei of the brain for different cranial reflexes, such as turning the eyes in response to a cutaneous stimulation on the hand. But their final terminus is in the thalamus, and after a synapse here the nervous impulse may be carried forward to the cerebral cortex by neurons of the third order. The spinal lemniscus system is the chief ascending pathway for nervous impulses giving rise to consciousness of touch, temperature, and pain from the trunk and limbs. There is a similar but anatomically distinct pathway to the thalamus for cutaneous sensibility from the head,

which is called the trigeminal lemniscus (see p. 197 and Figs. 64, 77, 81).

Within the spinal cord the nerve-fibers of sensibility to pressure, pain, and temperature run in three distinct tracts of the spinal lemniscus (the pain and temperature tracts very close together, see Figs. 59, 63, and 81), so that it occasionally happens that one may be destroyed by accident or disease without affecting the other two. Thus, at the level of the fifth cervical vertebra the destruction of the pathway for touch and pressure (tractus spino-thalamicus ventralis of Fig. 59) would result in the total loss of both cutaneous and deep sensibility to pressure over the whole of the opposite side of the body below the level of the injury, but there would be no disturbance of either temperature or pain sensibility. Similarly, by an injury of the tractus spino-thalamicus lateralis, pain or temperature sensibility might be lost with no disturbance of pressure sense. (For the description of a case of this sort see p. 191.)

Such combinations of symptoms as just described could not occur from any form of injury to the peripheral nerves, for in these nerves the various kinds of fibers are all mingled in the larger trunks, so that one functional component cannot be injured without involvement of the others also. And at the first division of these trunks into deep and superficial branches each branch also carries all or nearly all of the functional systems (see pp. 84–90).

The return pathway for motor nervous impulses from the cerebral cortex is the cortico-spinal tract or pyramidal tract (Fig. 64), whose fibers descend without interruption from the precentral gyrus of the cerebral cortex (see p. 318) to the spinal cord, where they form the lateral and ventral cortico-spinal tracts (Fig. 59). The various reflex centers of the brain stem also send motor fibers downward into the cord for the excitation of movements of the trunk and limbs. The tecto-spinal tract (Fig. 59) is such a path, leading from the optic and acoustic centers of the midbrain, as is also the vestibulo-spinal tract, leading from the vestibular nuclei of the medulla oblongata (p. 194, Fig. 83, neuron 16).

Summary.—The spinal nerves are segmentally arranged and are named after the vertebræ adjacent to which they emerge

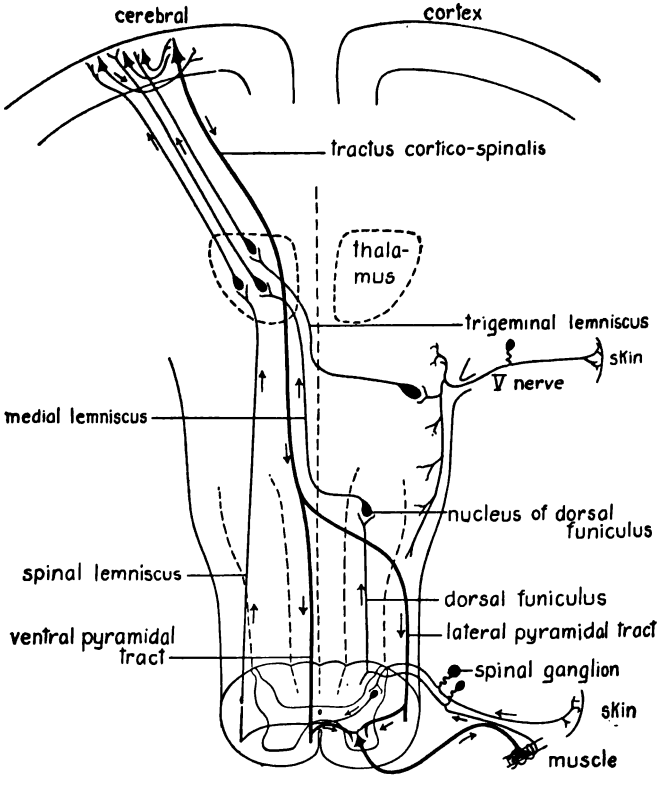

Fig. 64.—Diagram of the chief connections between the spinal cord and the cerebral cortex. The spinal lemniscus complex carries the ascending exteroceptive systems (touch, temperature, and pain); the dorsal funiculus and medial lemniscus complex carries chiefly ascending proprioceptive systems (a nerve of muscle sense is the only member of this group included in the drawing). The diagram also includes the sensory path from the skin of the head to the cerebral cortex through the V cranial nerve (trigeminus) and the trigeminal lemniscus (p. 171). The pyramidal tract (tractus cortico-spinalis) is the common descending motor path for both exteroceptive and proprioceptive nervous impulses from the cerebral cortex.

from the spinal canal of the vertebral column. Each nerve arises by a series of dorsal rootlets afferent in function and a series of ventral rootlets efferent in function. Most of the gray matter of the spinal cord is massed in two longitudinal columns on each side, for somatic sensory and somatic motor functions respectively. These are separated by an intermediate region containing the visceral sensory and motor centers and various correlation neurons. The white matter of the cord is superficial to the gray and contains myelinated fibers for various kinds of correlation, besides root-fibers of the spinal nerves. The white matter is divided topographically into funiculi and fasciculi and physiologically into tracts. The latter are the really significant units in the analysis of the cord. Peripherally, the spinal nerves divide into deep and superficial branches, and each of these contains various functional systems of fibers. As soon as the peripheral nerve-fibers have entered into the spinal cord they are segregated into proprioceptive and exteroceptive groups, and each of these again into particular functional tracts. There are connections for local spinal reflexes, reflexes of the brain stem and cerebellum, and for the cerebral cortex. The spino-cerebellar tracts and the dorsal funiculi are proprioceptive in function, and the spinal lemniscus carries spino-thalamic tracts of the systems of touch, temperature, and pain sensibility for the cerebral cortex. (See further in Chapter XI.)

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CHAPTER IX

THE MEDULLA OBLONGATA AND CEREBELLUM

THE brain contains a series of primary sensory and motor centers related to the cranial nerves and to their respective end-organs (see p. 117), the correlation mechanism which serves to connect these sensori-motor centers in working reflex systems, and an extensive system of conduction pathways between the brain and spinal cord and between the various correlation centers of the brain itself to serve the more complex systems of correlation and integration.

The brain is divided into two principal parts by a constriction in front of the cerebellum and pons, the isthmus (see p. 130). Above this level lies the cerebrum and below it the rhombencephalon, comprising the medulla oblongata or bulb and the cerebellum. The medulla oblongata contains the primary centers concerned with most of the simpler cerebral reflexes, especially those of the visceral, general cutaneous, auditory, and proprioceptive systems (see pp. 118–121). The cerebellum is a suprasegmental apparatus developed phylogenetically and embryologically out of the more primitive bulbar nuclei of the vestibular nerve, *i. e.*, out of the acoustico-lateral area of fishes (Figs. 43 and 44, pp. 119, 120, and Fig. 68; see also Herrick, 1914a).

The olfactory nerve (I pair), the so-called optic nerve (II pair), and the auditory nerve (VIII pair) are special sensory nerves, whose central connections will be described more in detail below. The remaining nine pairs of cranial nerves of the human body may be briefly summarized as follows:

The oculomotor nerve (III pair), trochlear nerve (IV pair), and abducens (VI pair) contain the somatic motor fibers and fibers of muscle sense related to the six muscles which move the eyeball. The III pair also contains visceral motor fibers for the ciliary ganglion, from which are innervated the muscles of the ciliary process and iris within the eyeball, *i. e.*, the muscles of accommodation and those which contract the

pupil. The trigeminal nerve (V pair) supplies general sensibility to the skin and deep tissues of the face and the motor innervation of the muscles of mastication. The facial nerve (VII pair) innervates the taste-buds of the anterior two-thirds of the tongue (special visceral sensory fibers), the sublingual and submaxillary salivary glands (general visceral efferent fibers), and the muscles related with the hyoid bone and the superficial facial muscles or muscles of facial expression, these two groups of muscles belonging to the series of special visceral muscles (p. 98). The glossopharyngeal nerve (IX pair) supplies fibers to the taste-buds on the posterior third of the tongue (special visceral sensory), also general sensibility to this region, motor fibers for the stylopharyngeus muscle (special visceral motor), and excito-glandular fibers for the parotid salivary gland (general visceral efferent). It also coöperates with the vagus nerve in innervating the skin about the external auditory canal (by the auricular branch of the vagus). The vagus nerve (X pair) is very complex. In addition to the general somatic sensory fibers of the auricular branch, which have just been mentioned, it contains general visceral sensory fibers from the pharynx, lungs, stomach, and other abdominal viscera, and visceral efferent fibers of several sorts to the pharynx, esophagus, stomach, intestines, lungs, heart, and arteries. The peripheral and central courses of most of these functional systems have been accurately determined, but are far too complex for summary here. The accessory nerve (XI pair) contains two parts: (1) the bulbar part, which should be regarded as nothing other than detached filaments of the vagus, for all of these fibers peripherally join vagus branches, (2) the spinal part, which arises by numerous rootlets from the upper levels of the spinal cord and participates in the innervation of two of the muscles of the shoulder (the trapezius and sternocleidomastoid muscles). The human hypoglossus nerve (XII pair) is a modified derivative of the first spinal nerve of lower vertebrates. It has lost its sensory fibers and innervates a special part of the tongue musculature. All of the nerves of the preceding list except the I, II, III, and IV pairs connect with the medulla oblongata.

For the details of the arrangement of the cranial nerves and their cerebral centers the larger manuals of neurology must be consulted. Here we have space for only a brief summary of some of the general principles which may assist in organizing these intricate anatomical facts in more comprehensible form.

The cranial nerves are usually described in our text-books as if they were segmental units like the spinal nerves (see p. 135). This was, in fact, the primitive condition which is still fairly obvious in the motor roots and nuclei (see Fig. 71); but in all vertebrate animals this segmental pattern has been greatly modified in such a way as to facilitate the discharge into the brain of all sensory fibers of like physiological type into a single center. The sensory roots and centers, accordingly,

do not show so clearly the primitive segmental pattern (Fig. 71). These physiological systems of fibers of like functional type are, therefore, the most useful units of structure in the cranial nerves. Each cranial nerve may contain several of these functional systems, and no two pairs of cranial nerves have the same composition. The components of the cranial nerves, like those of the spinal nerves (p. 136), are named in accordance with the same physiological criteria as their end-organs (see pp. 84–99).

A *functional system* may be defined as the sum of all the neurons in the body which possess certain physiological and anatomical characters in common so that they may react in a common mode. Morphologically, each system of peripheral nerves is defined by the terminal relations of its fibers—by the organs with which they are related peripherally and by the centers in which the fibers arise or terminate. A single peripheral nerve may contain several of these systems. It becomes necessary, therefore, to analyze the root complex of each pair of spinal and cranial nerves into its components, and to trace not only the central connections of these components within the spinal cord and brain, but also their peripheral courses as well. In other words, the description of any given nerve or ramus is not complete when we have given its point of origin from the nerve-trunk, root, or ganglion, the details of its devious courses, and the exact points where the several ramuli terminate. In addition to this it is necessary to learn what functional systems are represented in each ramus and the precise central and peripheral relations of each system.

The functional systems of peripheral nerve-fibers are so arranged in the cranial nerves as to suggest a rough grouping of the nerves and of their related primary centers in terms of the peripheral apparatus innervated. Thus in man, as in fishes (pp. 120, 132), the olfactory organ is related by means of the olfactory nerve with special olfactory centers which are described in Chapter XV.

The eyes are similarly connected by the II pair of nerves with optic centers (Chapter XIV), with which are intimately related the eye-muscle nerves (III, IV and VI pairs). The skin and muscles of the face and the facial skeleton are inner-

vated chiefly by the V and VII pairs, and the part of the brain with which these nerves connect may be called the facial part of the medulla oblongata (see p. 131). Next follows the VIII pair of nerves, connecting the internal ear with the highly specialized vestibular and cochlear nuclei. Finally, the lower part of the medulla oblongata (myelencephalon of the B. N. A., p. 130) is dominated by the visceral connections of the IX, X and XI pairs, and this region might well be called the visceral part of the medulla oblongata.

The Doctrine of Nerve Components.—The physiological analysis of the spinal nerves is diagrammatically indicated in Fig. 56 (p. 136), this pattern being segmentally repeated with minor variations throughout the length of the spinal cord (Fig. 41, p. 115).

The functional distinction between the dorsal (sensory) and the ventral (motor) roots of the spinal nerves is known as Bell's law. In reality, however, Sir Charles Bell's analysis was more like our current conception of the composition of the spinal and cranial nerves than is commonly recognized; for he identified not only the somatic sensory and somatic motor components but also the visceral components. The experimental researches of Bell more than a century ago were carried out in a comparative spirit and laid the foundation for the analysis of the functional composition of the nerves and their spinal and cerebral centers. An excellent popular account of these researches will be found in the introductory pages of Bell's Bridgewater Treatise (1885, pp. xi–xxxv). See also Bell (1811) and (1844). Many years later Gaskell (1886, 1889) gave a more explicit account of the visceral components which, however, differs considerably from that now in use.

The knowledge of the composition of the cranial nerves was long retarded by persistent attempts to analyze them in accordance with the analogy of a supposed simple spinal pattern. The typical spinal nerve according to the present conception contains two great groups of fibers, the somatic and the visceral, each with afferent and efferent subdivisions. The somatic group is concerned with the adjustment of the body to the outside world; the visceral group is concerned with the mechanisms of circulation, nutrition, etc., and its connections are made through the sympathetic nervous system (p. 251).

The somatic efferent fibers pass directly from their cell bodies in the ventral gray column of the spinal cord through the ventral roots to end upon the fibers of the skeletal muscles. The somatic afferent fibers are processes of neurons of the spinal ganglia. The somatic motor and sensory fibers of the cranial nerves are organized in essentially the same way as just described.

The visceral fibers of the spinal nerves are chiefly efferent in function. These efferent fibers arise from the intermedio-lateral column of gray in the spinal cord. They do not reach their terminal organs (smooth muscles, glands, etc.) directly, but always end in some sympathetic ganglion, with whose cells they effect functional connection. The impulse is then carried on to the peripheral organ by axons of these sympathetic neurons. The first of these elements, whose cell body lies within

the cord, is called the preganglionic neuron; the second is the postganglionic neuron.

The visceral sensory fibers of the spinal nerves are relatively few in number. Some such fibers arise from cell bodies of the spinal ganglia, whose peripheral processes distribute through the sympathetic nervous system to mucous surfaces, etc., and whose central processes enter the spinal cord through the dorsal roots. Other sensory fibers are supposed to arise from cell bodies in the sympathetic ganglia, but of these we have less positive information.

The cranial nerves exhibit a much more complex and diversified pattern than do the spinals. Their primary segmentation is obscure and there is still some difference of opinion as to the segmental relations of the twelve pairs as now commonly enumerated. These twelve pairs are convenient anatomical units, but for physiological and clinical purposes a much more useful unit is the functional system as defined above.

The analysis of these functional systems has been successfully accomplished by physiological experiment, microscopic reconstructions from serial sections, and other methods in representatives of many groups of vertebrates, and the general pattern is found to be tolerably uniform throughout (see the works by Johnston (1906 and 1909) cited in the appended bibliography for summaries of some of this literature).

Each of the four primary divisions of the spinal nerves (somatic sensory and motor, visceral sensory and motor, see p. 136) is represented in the head region in the same primitive unspecialized form as seen in the spinals, and also by specialized systems found only in one or more cranial nerves. This gives eight groups of functional systems represented in the cranial nerves, as follows:

1. General somatic afferent nerves, supplying (1) general exteroceptive sensibility to the skin and the underlying tissues, and (2) deep proprioceptive sensibility to the muscles, tendons, etc. Type 1 is represented in the V, IX, and X nerves, and in some lower vertebrates in the VII nerve also (Rhinehart, 1918, has shown that this is present in the mouse; there is some clinical evidence for its presence in the VII nerve of man); Type 2 is represented in the III, IV, V, VI nerves and probably in some of the others also.

2. Special somatic afferent nerves, for the innervation of highly differentiated sense organs. Here belong in the exteroceptive series the cochlear branch, and in the proprioceptive series the vestibular branch of the VIII pair. The lateral line nerves of fishes belong here, and probably the visual organ connected with the II pair in all vertebrates (though the so-called optic nerve is not a true nerve, see p. 230).

3. General somatic efferent nerves, supplying the general skeletal musculature of the body. In fishes this system is represented in several cranial nerves in addition to the spinalis, but in man it is lost in the cranial nerves, unless, as some believe, a part of the fibers of the XI pair belong here.

4. Special somatic efferent nerves, supplying two groups of highly specialized somatic muscles, namely, the external eye muscles and a part of the tongue muscles. They arise from a ventro-medial series of motor nuclei and are represented in the III, IV, VI, and XII pairs.

TABLE OF CRANIAL NERVE COMPONENTS

Nerves.	Components.	Chief Functions.	Cells of Origin.	Nerve Roots.	Chief Branches.
I.....	Special visceral and somatic afferent	Smell	In nasal mucous membrane	Fila olfactoria	
II.....	Special somatic afferent	Vision	In retina	.....	Not a true nerve
III.....	Special somatic efferent	Movement of eyeball	III nucleus	III root	Branches to mm. rectus sup., rectus inf., rectus med., obliquus inf., levator palpebræ superior.
	General visceral efferent	Intrinsic muscles of eyeball	Nucleus of Edinger-Westphal	III root	Preganglionic fibers to g. ciliare; postganglionic fibers in ciliary nerves
	Proprioceptive	Muscle sense of eye muscles	?	III root	Fibers mingled with motor fibers to four eye muscles
IV.....	Special somatic efferent	Movement of eyeball	IV nucleus	IV root	Nerve of m. obliquus superior
	Proprioceptive	Muscle sense	?	IV root	Sensory fibers to m. obliquus superior
V.....	Special visceral efferent	Movement of jaws	Motor V nucleus	Portio minor V	By n. mandibularis to temporal, masseter, ext. and int. pterygoid, tensor palati, tensor tympani, anterior belly of digastric and mylohyoid muscles
	General somatic afferent	Gen. sens. skin of head, nose, teeth, mouth, meninges	G. semilunare (Gasseri)	Portio major V	N. ophthalmicus, n. maxillaris, n. mandibularis
	Proprioceptive	Muscular sens. of jaw muscles	Nuc. mesencephalicus V ?	Portio major V	Fibers distribute with muscular branches of V
VI.....	Special somatic efferent	Movement of eyeball	VI nucleus	VI root	Nerve of m. rectus lateralis
	Proprioceptive	Muscle sense	?	VI root	Sensory fibers to m. rectus lateralis
VII.....	General visceral efferent	Secretion of saliva	Nuc. salivatorius superior	Portio intermedia	Preganglionic fibers in chorda tympani; postgang. fibers from submaxillary gang. to submaxillary and sublingual glands
	Special visceral efferent	Hyoid and facial musculature	Motor VII nucleus	Portio dura	Stapedius, posterior belly of digastric, stylohyoid, auricular and scalp muscles and superficial facial musculature
	General visceral afferent	Deep visceral sensibility	G. geniculi	Portio intermedia	Probably in all branches of facialis
	Special visceral afferent	Taste on anterior part of tongue	G. geniculi	Portio intermedia	Chorda tympani
	General somatic afferent	Cutaneous sens. of external ear	G. geniculi	Portio intermedia	Present in mouse, probably in man

VIII....	Proprioceptive	Equilibration and static sense	G. vestibulare	Radix vestibularis	Nervus vestibuli
	Special somatic afferent	Hearing	G. spirale	Radix cochlearis	Nervus cochleæ
IX.....	General visceral efferent	Secretion of saliva	Nuc. salivatorius inferior	Motor IX root	Preganglionic fibers in tympanic and small superf. petrosal nerves; postganglionic from otic ganglion to parotid gland
	Special visceral efferent	Movement of pharynx	Nuc. ambiguus	Motor IX root	Ramus stylopharyngeus IX
	General visceral afferent	Gen. sens. of pharynx and tongue	G. petrosum IX	Sens. IX root	Pharyngeal, lingual, and tympanic branches of IX and various sympathetic connections
	Special visceral afferent	Taste on posterior part of tongue	G. petrosum IX	Sens. IX root	Ramus lingualis IX
	General somatic afferent	Cutaneous sens. of external ear	G. superius IX	Sens. IX root	Joins r. auricularis vagi
X.....	General visceral efferent	Unstriped muscles and glands of gut and other viscera	Dorsal mot. nuc. of X	Motor X	Rami for pharynx, esophagus, stomach, heart, lungs, etc., via sympathetic system (preganglionic fibers)
	Special visceral efferent	Muscles of pharynx and larynx	Nuc. ambiguus	Motor X	Superior and inferior laryngeal and pharyngeal nerves
	General visceral afferent	Visc. sensation of pharynx, thorax, and abdomen	G. nodosum	Sensory X	Rami from pharynx, esophagus, stomach, heart, lungs, etc., and various symp. connections
	Special visceral afferent	Taste in region of epiglottis	G. nodosum	Sensory X	Probably in internal laryngeal nerve
	General somatic afferent	Cutaneous sens. of external ear	G. jugulare X	Sensory X	Ramus auricularis vagi
XI.....	Special visceral efferent	A. striated muscles of pharynx	Nuc. ambiguus	In cerebral roots of XI	To striated muscles of the pharynx accompanying vagus branches
		B. movement of shoulder	Lateral column of spinal cord	In spinal roots of XI	Rami to trapezius and sternocleidomastoid muscles
XII.....	Special somatic efferent	Movement of tongue	XII nucleus	XII roots	Hypoglossus nerve
Spinal nerves	General somatic efferent	Skeletal muscles	Ventral gray column	Ventral root	Muscular branches
	General visceral efferent	Visceral muscles and glands	Lateral gray column	Ventral root	Preganglionic fibers in rami communicantes to sympathetic ganglia
	General somatic afferent	Cutaneous and deep sensibility	Spinal ganglion	Dorsal root	Cutaneous and deep nerves
	General visceral afferent	Visceral sensibility	Spinal ganglion	Dorsal root	Various sympathetic connections through rami communicantes

The nervus terminalis is a slender nerve associated with the I pair in vertebrates generally, from fishes to man (see Fig. 43, p. 119, and p. 241). Its physiological and morphological relations are obscure; it is, accordingly, omitted from the table. Proprioceptive fibers are probably present in nerves VII, IX, X, XI, and XII, but their courses are unknown.

5. General visceral afferent nerves, innervating visceral mucous surfaces without highly differentiated sense organs. They distribute through the sympathetic nervous system and are represented in the VII, IX, and X pairs and perhaps in some others.

6. Special visceral afferent nerves, for the innervation of specialized sense organs serving the senses of taste and smell. The gustatory fibers are represented in the VII, IX, and X pairs. The olfactory nerve (I pair) is probably a more highly differentiated member of this group (see pp. 97 and 241).

7. General visceral efferent nerves, for unstriped involuntary visceral muscles, heart muscle, glands, etc., distributing through the sympathetic nervous system. These fibers (preganglionic fibers of Langley, p. 258) are present in the III, VII. IX, and X pairs.

8. Special visceral efferent nerves, supplying highly specialized striated muscles of a different origin (both embryologically and phylogenetically) from the striated trunk muscles. These muscles are connected with the visceral or facial skeleton of the head and are derived from the gill muscles of fishes. These nerves in the adult body resemble those of the somatic motor system, save that they arise from a different series of motor nuclei in the brain (the ventro-lateral motor column). They have no connection with the sympathetic nervous system and are represented in the V, VII, IX, X, and XI pairs.

In the preceding Table of Nerve Components (pages 160, 161) the several cranial nerves are analyzed and compared with a typical spinal nerve.

The various functional systems of the head tend to be concentrated in one or a few cranial nerves for ease of central correlation, and even in case a given system is represented in several nerves, the fibers of this system may converge within the brain to connect with a compact center. This is well illustrated by the gustatory and acoustico-lateral systems of the cranial nerves of the fish, Menidia, as shown in Fig. 65. Here the gustatory system (indicated by cross-hatching) is present in the VII, IX, and X cranial nerves, and all of these fibers, together with other visceral fibers, converge within the brain to enter the visceral sensory area in the vagal lobe (*lob. X.*). Similarly, the lateral line components of the VII and X nerves and the VIII (printed in solid black) converge to enter the acoustico-lateral area (formerly called the tuberculum acusticum, *t.a.*). The general cutaneous fibers enter by the V and X nerves, and all of these fibers enter the spinal V tract (*sp.V.*).

In the paragraphs which follow the chief central connections (terminal nuclei of the sensory systems and nuclei of origin of the motor systems, see p. 116) of some of the cranial nerve components are summarized (see

Fig. 71). For the details of these connections the larger text-books of neurology should be consulted.

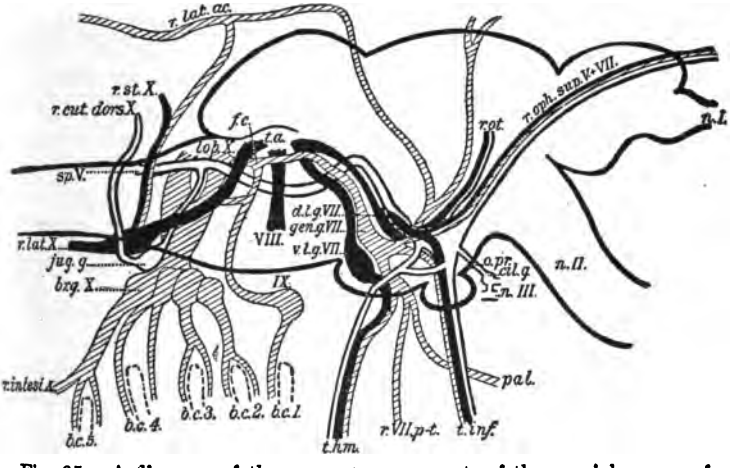


Fig. 65.—A diagram of the sensory components of the cranial nerves of a fish, Menidia. The brain is outlined as seen from the right side with heavy black lines. The general cutaneous nerves (somatic sensory) are outlined with finer lines (unshaded), and all of these fibers are seen to enter a longitudinal tract within the brain, the spinal trigeminal tract (*sp.V.*). The special somatic sensory (acoustic and lateral line) nerves (black) converge within the brain to a special center, the acoustico-lateral area (*t.a.*). The visceral sensory fibers (cross-hatched) likewise all converge to a special center, the lobus vagi (*lob.X.*).

Reference letters: *b.c.*1 to *b.c.*5, gill clefts; *br.g.X.*, branchial ganglia of X nerve; *cil.g.*, ciliary ganglion; *d.l.g.VII.*, dorsal lateral line ganglion of VII nerve; *f.c.*, fasciculus solitarius; *gen.g.VII.*, geniculate ganglion of VII nerve; *IX.*, glossopharyngeal nerve; *jug.g.*, jugular ganglion of X nerve; *lob.X.*, lobus vagi (visceral sensory area); *n.I.*, olfactory nerve; *n.II.*, optic nerve; *n.III.*, oculomotor nerve; *o.pr.*, ramus ophthalmicus profundus; *pal.*, palatine branch of VII nerve; *r.cut.dors.X.*, dorsal cutaneous branch of X nerve; *r.intest.X.*, intestinal branch of X nerve; *r.lat.ac.*, ramus lateralis accessorius of VII nerve; *r.lat.X.*, lateral line branch of X nerve; *r.oph.sup.V.+VII.*, superficial ophthalmic branch of V and VII nerves; *r.ot.*, ramus oticus; *r.st.X.*, supratemporal branch of X nerve; *r.VII.p-t.*, pretrematic branch of VII nerve; *sp.V.*, spinal trigeminal tract; *t.a.*, acoustico-lateral area; *t.hm.*, hyomandibular trunk; *t.inf.*, infraorbital trunk; *VIII.*, auditory nerve; *v.l.g.VII.*, ventral lateral line ganglion of VII nerve.

1. *General Cutaneous System* (part of the general somatic afferent, represented in the V, IX, and X nerves).—Chief sensory V nucleus and spinal V nucleus, or gelatinous substance of Rolando of the medulla oblongata.

2. *Special Somatic Afferent Systems.*—(1) Vestibular nuclei; (2) cochlear nuclei; (3) optic tectum in the colliculus superior, optic part of the thalamus (lateral geniculate body and pulvinar); (4) olfactory bulb (the olfactory nerve and its cerebral centers combine somatic and visceral functions).

3. *General Somatic Efferent System.*—Not represented in the human cranial nerves.

4. *Special Somatic Efferent Systems* (III, IV, VI, and XII nerves).—A series of ventral motor nuclei in the midbrain and medulla oblongata.

5 and 6. *General and Special Visceral Afferent Systems* (VII, IX, and X nerves).—All of the fibers concerned with general visceral sensibility and taste enter a single longitudinal tract, the fasciculus solitarius, and terminate in the nucleus which accompanies this fasciculus. The olfactory nerve and its cerebral centers (in part) should also be included here.

7. *General Visceral Efferent Systems* (III, VII, IX, and X nerves).—These are preganglionic fibers of the sympathetic system and arise from laterally placed nuclei (except that of the III nerve, which is joined to the ventral somatic motor nucleus).

8. *Special Visceral Efferent Systems* (V, VII, IX, X, and XI nerves).—A series of lateral motor nuclei of the medulla oblongata.

The spinal nerves, as we have seen, enter the spinal cord by a series of segmentally arranged roots. Within the spinal cord,

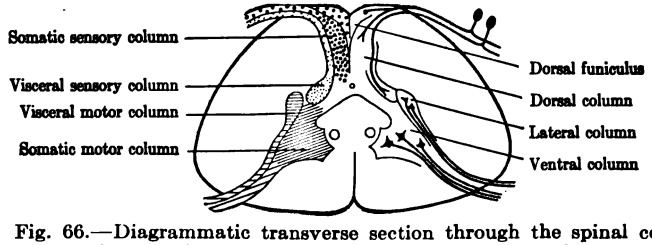


Fig. 66.—Diagrammatic transverse section through the spinal cord of a fish (Menidia) to illustrate the relations of the functional columns of the gray matter to the nerve roots. The relations of the visceral sensory component are problematical, and fibers of the visceral motor component probably emerge with the dorsal root, as well as with the ventral root, though only the latter are included in the diagram.

however, their components are rearranged in longitudinal columns which cut across and obscure the primary segmentation. The sensory root-fibers and their terminal gray centers occupy the dorsal part of the spinal cord and the motor roots and their centers the ventral part (Figs. 66 and 67). In the brain the same arrangement prevails, the sensory centers lying dorsal to the motor. In the cranial nerves, moreover, the four primary groups of functional systems of the peripheral nerves are more clearly differentiated than in the spinal nerves, and from this it follows that their primary centers are correspondingly highly

developed and distinct. The medulla oblongata, in fact, is divided into four longitudinal columns related respectively to the great primary groups of functional systems. In fishes, where the amount of correlation itssue is less than in man, these four primary columns appear as well-defined ridges in the wall of the fourth ventricle (see pp. 118–121).

An enlarged view of the medulla oblongata of the dogfish is seen in Fig. 68, which also illustrates the arrangements of the primary sensory and motor centers in cross-section at the level of the vagus nerve. Figure 69 shows a cross-section through the medulla oblongata in the region of the vagus nerve in another fish, the sea-robin. In all of these cases the four principal func-

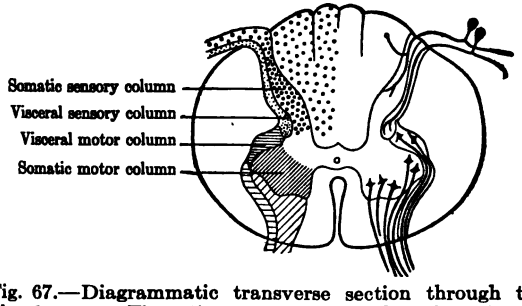
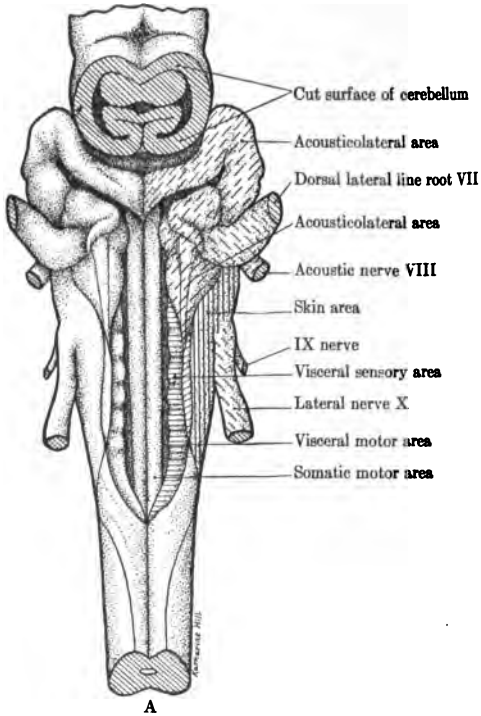


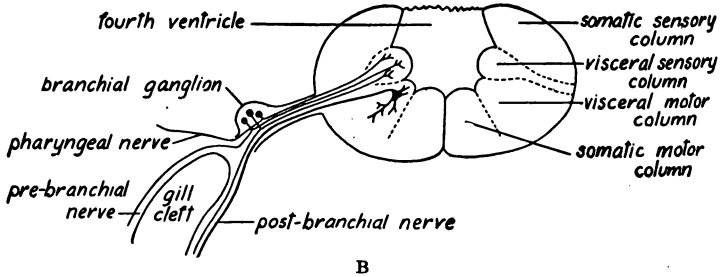
Fig. 67.—Diagrammatic transverse section through the human spinal cord. Compare Figs. 56 to 59 and note the relatively greater size of the dorsal gray columns and dorsal funiculi in man than in the fish (Fig. 66). This is correlated with the greater importance in man of the ascending connections between the cord and the brain (see p. 139).

tional systems (see pp. 81 and 84–99) are arranged in longitudinal columns from the dorsal to the ventral surface in the order: somatic sensory, visceral sensory, visceral motor, and somatic motor centers, as indicated diagrammatically on the left side of Fig. 69. The arrangement of the peripheral nerve-fibers of these systems is indicated on the right side. Figure 70 illustrates a cross-section through the corresponding region of the medulla oblongata in an early human embryo, where the same general arrangement of the sensorimotor centers is evident.

Figure 71 gives a view of the adult human medulla oblongata and midbrain after the removal of the cerebellum and mem-



A



B

Fig. 68.—A. The medulla oblongata of the dogfish, Squalus acanthias, seen from above after removal of the membranous roof of the fourth ventricle and the posterior part of the cerebellum; × 2. On the right side the nerve roots and functional areas of the brain are indicated by the same conventional markings as in Figs. 43 and 44 (pp. 119 and 120).

B. Diagrammatic cross-section through the medulla oblongata of the dogfish in the region of the vagus nerve to illustrate the innervation of the gills and the arrangement of the functional columns of the oblongata. The groove between the visceral motor column and the visceral sensory column is the sulcus limitans (p. 125).

branous roof of the fourth ventricle. (For the form of the oblongata, as seen from below, see Fig. 53.) In this figure the

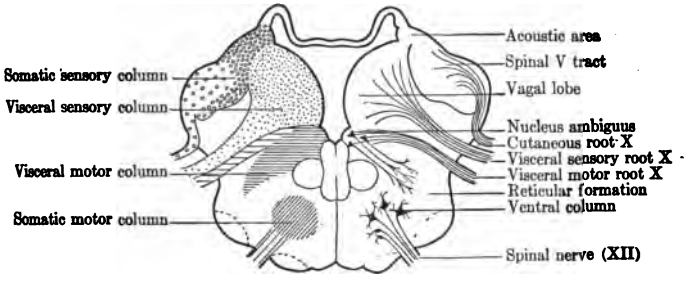


Fig. 69.—Diagrammatic cross-section through the medulla oblongata at the level of the vagus nerve in a bony fish (the sea-robin, Prionotus carolinus), to illustrate the arrangement of the four principal functional columns.

positions of the primary sensory and motor nuclei are drawn as projected upon the dorsal surface, the motor centers on the left and the sensory centers on the right. The somatic motor

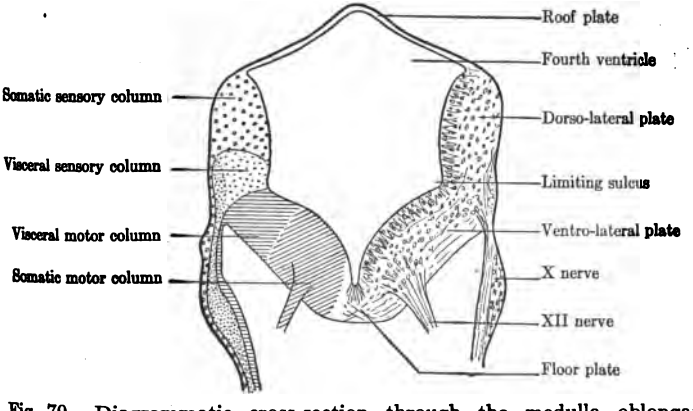


Fig. 70.—Diagrammatic cross-section through the medulla oblongata at the level of the vagus nerve of a human embryo of 10.2 mm. (fifth week), to illustrate the arrangement of the four principal functional columns. (Compare Fig. 69.)

nuclei are indicated by circles, the general visceral motor nuclei by small dots, the special visceral motor nuclei by large dots, the visceral sensory nuclei by double cross-hatching, the

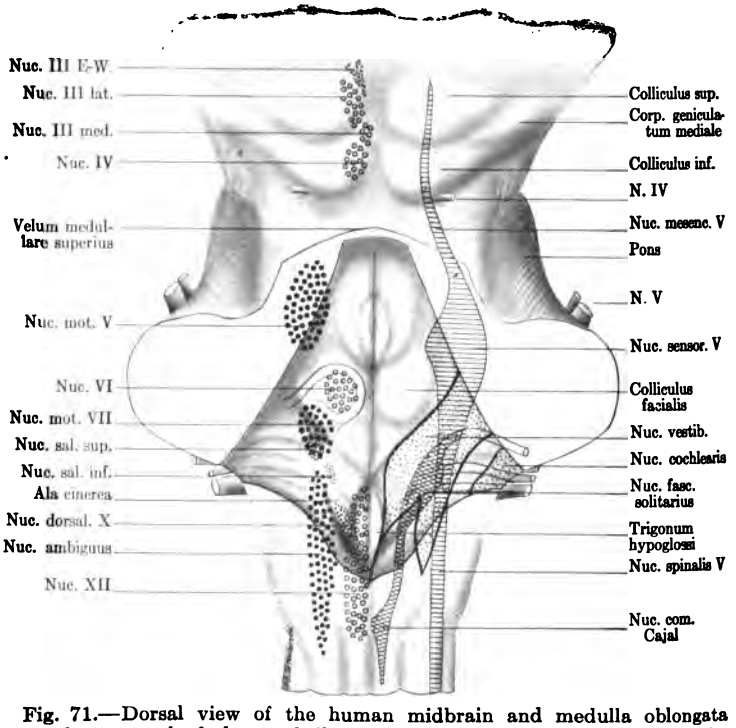


Fig. 71.—Dorsal view of the human midbrain and medulla oblongata after the removal of the cerebellum and the roof of the fourth ventricle, with the positions of the cranial nerve nuclei projected upon the surface. The motor nuclei are indicated on the left side and the sensory nuclei on the right. The somatic motor nuclei are indicated by circles, the general visceral efferent nuclei by small dots, and the special visceral efferent nuclei by large dots. The general somatic sensory area is indicated by horizontal lines, the visceral sensory area by double cross-hatching, and the special somatic sensory area by open stipple. (Compare Figs. 77, 86, and 114.)

n.IV, nervus trochlearis; *nuc.com.Cajal*, the commissural nucleus of Ramón y Cajal; *nuc.III E-W.*, the small-celled visceral motor nucleus of the III nerve, or nucleus of Edinger-Westphal; *nuc.III. lat.*, lateral nucleus of III nerve; *nuc. III med.*, medial nucleus of III nerve; *nuc.IV*, nucleus of IV nerve; *nuc.mesenc.V*, mesencephalic nucleus of V nerve; *nuc.mot.V*, motor nucleus of V nerve; *nuc.mot.VII*, chief motor nucleus of VII nerve; *nuc.sal. inf.*, nucleus salivatorius inferior; *nuc.sal.sup.*, nucleus salivatorius superior; *nuc.sensor.V*, chief sensory nucleus of V nerve; *nuc.VI*, nucleus of VI nerve; *nuc. XII*, nucleus of XII nerve; *n.V*, nervus trigeminus.

general somatic sensory nuclei by single cross-hatching, and the cochlear and vestibular nuclei (special somatic sensory) by open stipple bounded by heavy lines.

A more accurate mapping of the exact topographic relations between the superficial landmarks and the underlying deep structures has recently been published by Weed (Publications of the Carnegie Institution of Washington, No. 191, 1914), following an earlier and less complete study by Streeter. Miss Sabin has published detailed reconstructions

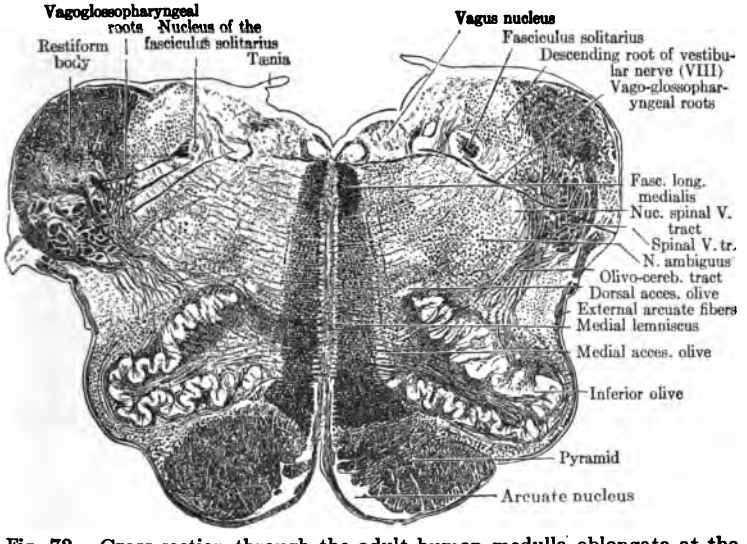


Fig. 72.—Cross-section through the adult human medulla oblongata at the level of the IX cranial nerve. (From Cunningham's Anatomy.)

(An Atlas of the Medulla and Midbrain, Baltimore, 1901) and a series of enlarged models of the internal anatomy of the brain stem of the newborn babe.

Figure 72 illustrates the appearance of a cross-section through the adult human medulla oblongata at the level of the roots of the IX nerve, and Fig. 73 presents an analysis of a section slightly nearer the spinal cord at the level of the X nerve. Figure 74 is a diagrammatic representation of the relations of the four principal functional systems at the same level as shown by Fig. 73 for comparison with Figs. 66, 67, 69, 70. It is obvious that, while the general relations in the human embryo (Fig. 70) resemble tolerably closely those of the adult fish (Fig. 69), in a human adult (Fig. 74) this primary arrangement has been greatly disturbed by the addition of many new tracts and centers in the ventral part of the cross-section.

We cannot here undertake an analysis of the complex reflex connections of the medulla oblongata. In general, each of the primary terminal nuclei of the sensory roots of the cranial

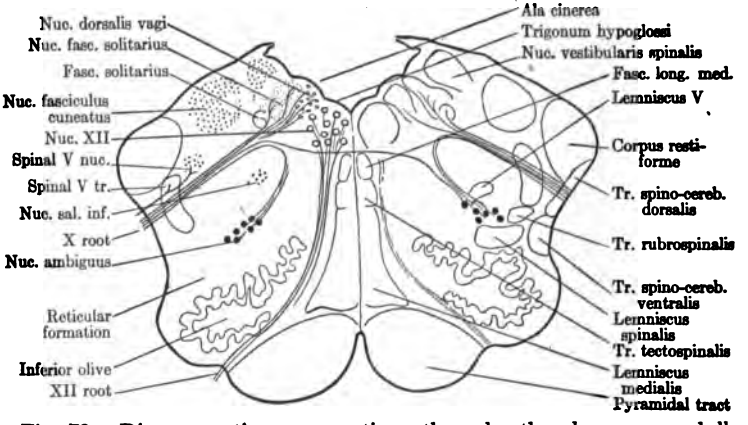


Fig. 73.—Diagrammatic cross-section through the human medulla oblongata at the level of the vagus nerve, illustrating details of functional localization in addition to those shown in Fig. 72.

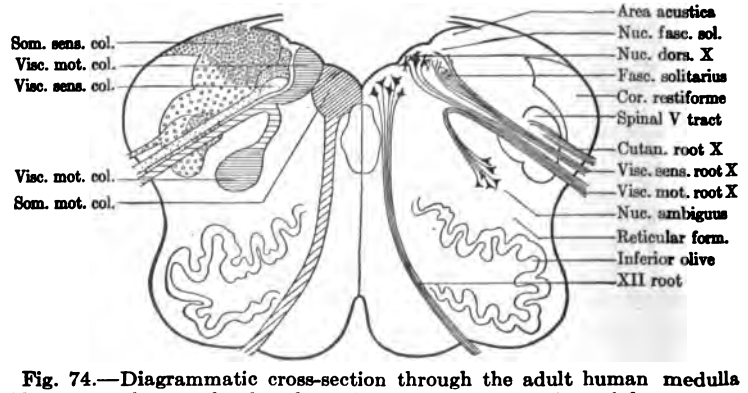


Fig. 74.—Diagrammatic cross-section through the adult human medulla oblongata at the same level as shown in Fig. 73, for comparison of the arrangement of the principal functional columns with that of Figs. 69 and 70.

nerves effects four types of connections: (1) direct reflex connections with the motor nuclei of the medulla oblongata, these connections being effected through the reticular forma-

tion (Figs. 69, 73); (2) descending reflex connections with the motor centers of the spinal cord, by way of the bulbo-spinal tracts (such as the vestibulo-spinal tract, Fig. 59); (3) connections with the cerebellum (this applies only to such functional systems as have proprioceptive value, of which the vestibular nerve from the semicircular canals of the ear is the most important); (4) connections with the thalamus and (after a synapse here) with the cerebral cortex.

The fibers of the last type mentioned comprise the bulbar lemniscus systems. A lemniscus may be defined as a central system of sensory fibers terminating in the thalamus. Its fibers are axons of neurons of the second order in the pathway between the peripheral sense organs and the cerebral cortex. The spinal lemniscus systems have already been described (p. 150). Of the bulbar lemniscus systems there are three which require special mention, viz., the trigeminal lemniscus, the lateral lemniscus and the medial lemniscus. The skin of the face is innervated chiefly by the trigeminal nerve (V pair) and the fibers of this type terminate in the general somatic sensory area (known as the chief sensory V nucleus and the spinal V nucleus or gelatinous substance of Rolando, Figs. 71–74). After a synapse in this area the fibers of the trigeminal lemniscus cross to the opposite side and ascend to the thalamus in a pathway distinct from all other lemniscus fibers (see p. 197 and Figs. 64, 75, 77, 78, 81).

The fibers of the lateral or acoustic lemniscus arise from the terminal nuclei of the cochlear nerve (VIII pair, Fig. 71), cross at once to the opposite side of the brain, and ascend to the midbrain (Fig. 75). Some of these fibers continue directly to the thalamus, where they end in the medial geniculate body (Fig. 77); others terminate in the roof of the inferior colliculus of the midbrain. After a synapse here and various reflex connections, the nervous impulse may be carried forward to the medial geniculate body of the thalamus by way of the brachium quadrigeminum inferius (Figs. 75, 86). (Regarding this system see further on pp. 219–228.)

The medial lemniscus or fillet carries proprioceptive impulses from the spinal cord to the thalamus (pp. 149, 193 and Figs. 64, 72 to 75, 77, 78, 83). Its fibers arise from the nucleus of the fasciculus gracilis and cuneatus at the extreme lower end

of the medulla oblongata, cross at once to the opposite side under the ventricle (decussation of the lemniscus), and then ascend directly to the thalamus.

In fishes there is an ascending secondary visceral and gustatory tract, or visceral lemniscus, from the visceral sensory area to the midbrain (p. 276 and Herrick, 1905); this tract no doubt occurs in the human brain also, though its exact course has never been demonstrated. Monakow (1913) has described a different connection in man, viz., a visceral lemniscus arising from large neurons lying ventrally and laterally of the nucleus of the fasciculus solitarius, entering the dorsal part of the medial lemniscus of the opposite side, and terminating in the ventrolateral nucleus of the thalamus.

Having now reviewed cursorily the primary sensory and motor centers of the medulla oblongata, we must next examine some of the centers of correlation. As has already been indicated, all of these centers are interconnected by correlation neurons similar to those of the spinal cord (Figs. 60, 61). These neurons are loosely arranged in the spaces between the sensory and motor groups of nuclei, this tissue being termed the *reticular formation* (this region is also called the tegmentum, see pp. 69, 137 and Figs. 69, 74). But the chief centers of correlation of the brain stem are found in specially enlarged nuclei of the midbrain and thalamus, some of which are mentioned in the next chapter.

In its more ventral parts the medulla oblongata contains a number of large correlation centers and important conduction pathways between remote parts of the brain. Of the former, the largest are the inferior olives (Figs. 72, 73, 74), deeply buried masses of gray matter arranged in the form of a hollow shell of complex shape on each side of the median plane. The olives receive fibers from the thalamus and spinal cord and discharge into the cerebellum (olivo-cerebellar fibers of Fig. 72). Their functions are unknown.

The *cerebellum* has already been referred to as a great suprasegmental mechanism of unconscious motor coördination. It is connected with the underlying brain stem by three pairs of stalks or peduncles, two of which join the medulla oblongata and one the midbrain. The inferior peduncle (restiform body) connects with the dorsal margin of the medulla oblongata and

carries fibers into the cerebellum from the spinal cord and oblongata. The middle peduncle (brachium pontis) connects with the pons and most of its fibers convey impulses from the nuclei of the pons to the cerebellum. The superior peduncle (brachium conjunctivum) connects with the tegmental region of the cerebral peduncle in the floor of the midbrain and contains chiefly fibers which descend from the cerebellum, cross the midplane under the aqueduct of Sylvius, and terminate in or near the red nucleus (Fig. 75, nucleus ruber). The internal structure and connections of the cerebellum will be further considered on page 205.

Summary.—The rhombencephalon includes the medulla oblongata and cerebellum, that is, all parts of the brain below the isthmus. All of the cranial nerves except the first four pairs connect with the medulla oblongata. An analysis of the functional components of the cranial nerves shows that they can best be understood by considering each functional system of fibers as a unit and studying the connections of each component separately. These connections are summarized in a table on pp. 160, 161. The medulla oblongata of lower vertebrates and of the human embryo is seen to be composed chiefly of the primary centers related to these functional components of the peripheral nerves, arranged in longitudinal columns in the order from dorsal to ventral surfaces on each side of somatic sensory, visceral sensory, visceral motor, somatic motor centers. The same arrangement appears in the adult human oblongata, though somewhat distorted by the presence of large masses of correlation tissue and of large conduction tracts which are not present in the lower vertebrates. The sensory centers of the oblongata are connected locally with the adjacent motor centers and also by longer tracts with the spinal cord, cerebellum, and thalamus. The latter fibers constitute the bulbar lemniscus, of which several functional components can be distinguished, the most important being the trigeminal lemniscus for general cutaneous sensibility, the lateral or acoustic lemniscus for auditory sensibility and the medial lemniscus for spinal proprioceptive sensibility. The cerebellum is a proprioceptive center developed out of the vestibular area of the medulla oblongata.

Literature

The details of the structure and functions of the parts mentioned in this and the following chapters will be found fully presented in the standard text-books of human anatomy and physiology and in the medical text-books of neurology, and all of this literature up to the year 1899 is summarized in Barker's Nervous System and Its Constituent Neurones. See also W. von Bechterew, Die Funktionen der Nervencentra, Jena, 1908 to 1911, 3 vols. and the books listed on page 14. For discussions of comparative neurology and the evolution of the nervous system, reference may be made to articles in the neurological journals, especially the *Journal of Comparative Neurology;* see also the Bibliographies on pp. 38, 134, 188, 217, and 250, and the following works:

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CHAPTER X

THE CEREBRUM

THE cerebrum includes all of the brain lying in front of the isthmus, that is, the midbrain (mesencephalon), betweenbrain (diencephalon), and cerebral hemispheres (telencephalon), the two last comprising the forebrain (prosencephalon). It contains the primary sensory centers of the olfactory nerves (I pair), the sensory correlation centers of smell and sight, the primary motor and sensory centers of the oculomotor and trochlear nerves (III and IV pairs) for movements of the eyes, and all of the most important higher correlation centers of the brain. These higher correlation centers make up by far the larger part of its substance in the human brain, though in fishes the converse relation prevails, with the primary sensorimotor centers and the simpler correlation mechanisms making up the larger part (see Figs. 43, 44, pp. 119, 120).

The *mesencephalon* (midbrain) is that part of the brain in which the early embryonic neural tube (Figs. 46–51, pp. 124–128) has been least modified in the adult. The ventral part of the midbrain, *i. e.*, the part lying ventrally of the ventricle, which is here termed the aqueduct of Sylvius, is called the cerebral peduncle; the dorsal part is the corpora quadrigemina, the upper pair of these four eminences being the superior colliculi, and the lower pair the inferior colliculi (see Fig. 71, p. 168).

The corpora quadrigemina contain important correlation centers, the superior colliculus chiefly visual (p. 234) and the inferior colliculus chiefly auditory (p. 227). The cerebral peduncle, as the name implies, contains the great ascending and descending fiber tracts between the forebrain above and the medulla oblongata, cerebellum, and spinal cord below. The arrangement of some of these tracts can be seen in Fig. 75. The cerebral peduncle also contains the nuclei of origin for the motor fibers of the III and IV pairs of cranial nerves and sev-

eral masses of gray matter devoted to motor coördination, such as the black substance (substantia nigra) and the red nucleus (nucleus ruber, see p. 207).

The *diencephalon* (betweenbrain or thalamencephalon) in early embryonic development is a transverse region of the simple neural tube (Fig. 48, p. 126) surrounding the third ventricle.

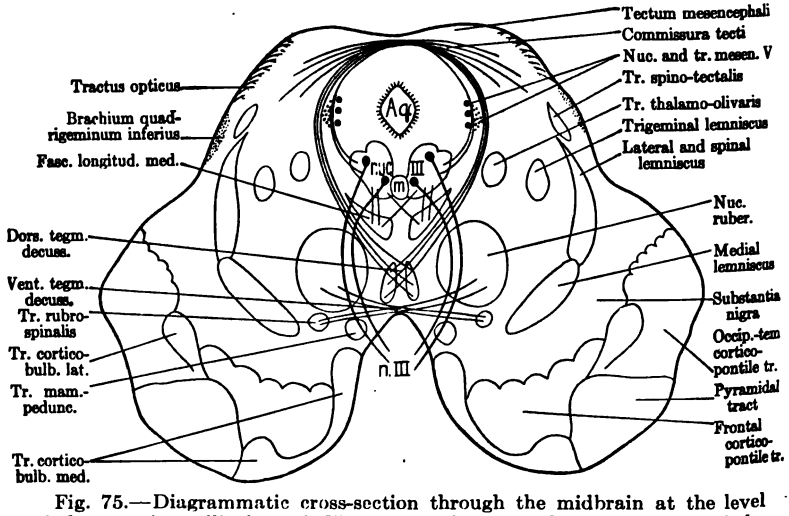

Fig. 75.—Diagrammatic cross-section through the midbrain at the level of the superior colliculus (cf. Fig. 71), to illustrate the arrangement of the chief conduction pathways: *aq.*, aqueduct of Sylvius; *m*, medial part of motor nucleus of oculomotor nerve; *n.III*, oculomotor nerve; *nuc.III*, motor nucleus of oculomotor nerve; *Tr.mam.-pedunc.*, tractus mamillo-peduncularis. The fibers of the dorsal tegmental decussation (*Dors. tegm. decuss.*, also known as the fountain decussation of Meynert) arise from the roof of the midbrain (tectum opticum) and immediately after crossing the median plane descend toward the spinal cord, where they form part of the tractus tecto-spinalis (Fig. 59, p. 140 and Fig. 73, p. 170). The fibers of the ventral tegmental decussation (*Vent.tegm.decuss.*, also known as Forel's decussation) in a similar way arise from the nucleus ruber and enter the opposite tractus rubro-spinalis.

In the adult human brain, however, it is entirely concealed by other parts. Its dorsal surface is exposed in the dissection shown in Fig. 76 (p. 177) and in the diagram, Fig. 77. The medial surface is seen in Figs. 51, 52 (p. 128). This part of the brain is devoted wholly to various types of correlation. It has three main divisions, the thalamus, the epithalamus, and the

hypothalamus, of which the last two are dominated by the olfactory apparatus (see p. 247).

The *epithalamus* consists of the membranous roof of the third ventricle (Figs. 76, 79), including the choroid plexus of the third ventricle (p. 133), the pineal body or epiphysis (Fig. 76),

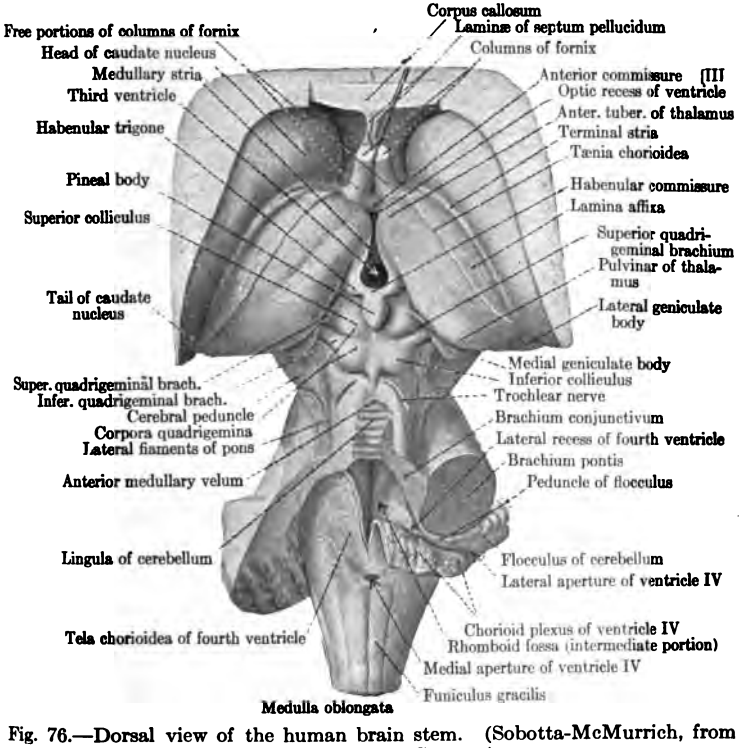

Fig. 76.—Dorsal view of the human brain stem. (Sobotta-McMurrich, from Ranson's Nervous System.)

the habenula (marked habenular trigone on Fig. 76), and the stria medullaris, a fiber tract which connects the olfactory centers of the cerebral hemispheres with the habenula (Figs. 76, 78, 79, 106). The habenula is a center for the correlation of olfactory sensory impulses with the various somatic sensory centers of the dorsal part of the thalamus. The pineal body of some

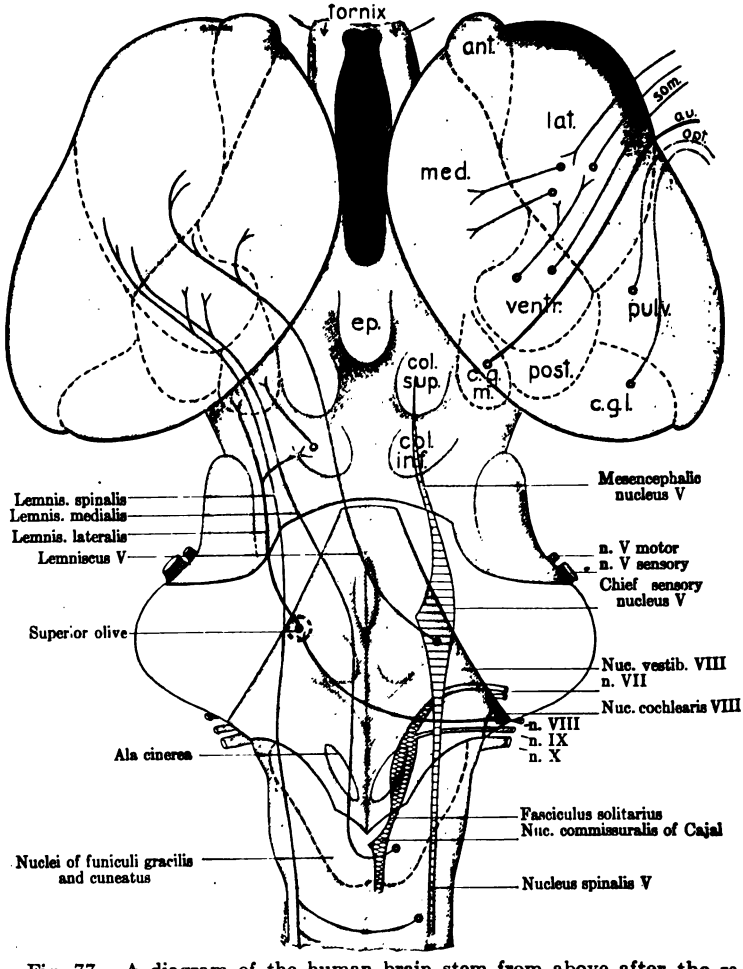

Fig. 77.—A diagram of the human brain stem from above after the removal of the cerebral hemispheres, to illustrate the nuclei of the thalamus and some of the chief fiber tracts connected with them. Compare Figs. 71 and 76. The fibers of the sensory radiations between the thalamus and the cerebral cortex fall into three groups: somesthetic (*som.*) for touch, temperature, and spatial discrimination, auditory (*au.*), and optic (*opt.*). Descending cortico-thalamic fibers are shown in connection with the somesthetic radiation only; but such fibers are present in the auditory and optic radiations also. *ant.*, anterior nucleus of thalamus; *ep.*, pineal body (epiphysis);

lower vertebrates is a sense organ, apparently visual in function and known as the parietal eye (p. 239); in man its primary sensory function is lost and it is said to produce an internal secretion whose physiological value is still obscure.

The *hypothalamus* includes the tuber cinereum and mammillary bodies (see Figs. 53, 78, 79, and 106), these structures being olfactory centers, and the hypophysis or pituitary body (which has been removed from the specimen shown in Fig. 53, its point of attachment being the infundibulum). The hypophysis is a glandular organ which produces an internal secretion of great importance in maintaining the proper balance of the metabolic activities of the body. The hypothalamus is an important center for the correlation of olfactory impulses with various visceral functions, including probably the sense of taste.

The *thalamus* is in the human brain chiefly a sort of vestibule through which the systems of somatic sensory nervous impulses reach the cerebral cortex. There are, however, two parts of the thalamus which should be clearly distinguished. The ventral part contains chiefly motor coördination centers. It is feebly developed in the human brain, where it is termed the subthalamus (not to be confused, as is often done, with the hypothalamus, see Figs. 78, 79, and 81). The dorsal part of the thalamus, in its turn, contains two distinct types of sensory correlation centers: (1) primitive sensory reflex centers, chiefly in the medial group of thalamic nuclei; (2) the more lateral nuclei which form the cortical vestibule to which reference was made above. These lateral nuclei are sometimes called the new thalamus (neothalamus) in distinction from all of the other thalamic nuclei which form the old thalamus (palæothalamus).

The centers which comprise the new thalamus make up by far the larger part of the thalamus in the human brain and include the following nuclei: the lateral, ventral, and posterior nuclei (for general cutaneous and deep sensibility) receiving the spinal, trigeminal, and medial lemnisci; the lateral geniculate

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c.g.l., corpus geniculatum laterale; *c.g.m.*, corpus geniculatum mediale; *col. inf.*, colliculus inferior; *col. sup.*, colliculus superior; *lat.*, lateral nucleus of thalamus; *med.*, medial nucleus of thalamus; *post.*, posterior nucleus of thalamus; *pulv.*, pulvinar; *ventr.*, ventral nucleus of thalamus. Root fibers of the X nerve, in addition to those of the VII and IX nerves, should be shown entering the fasciculus solitarius (cf. Fig. 114). Those of the VII and IX nerves are chiefly gustatory.

late body and pulvinar (visual sensibility) receiving the optic tracts; the medial geniculate body (auditory sensibility) receiving the lateral or acoustic lemniscus. The lateral and medial geniculate bodies comprise the metathalamus of the B. N. A. (see p. 129 and Fig. 50, p. 127), which in this work are described as part of the thalamus.

All of the thalamic nuclei of the lateral group (the neothalamus) are connected by important systems of fibers with the cerebral cortex, these fibers running both to and from the cortex (Fig. 77). These are called sensory projection fibers and

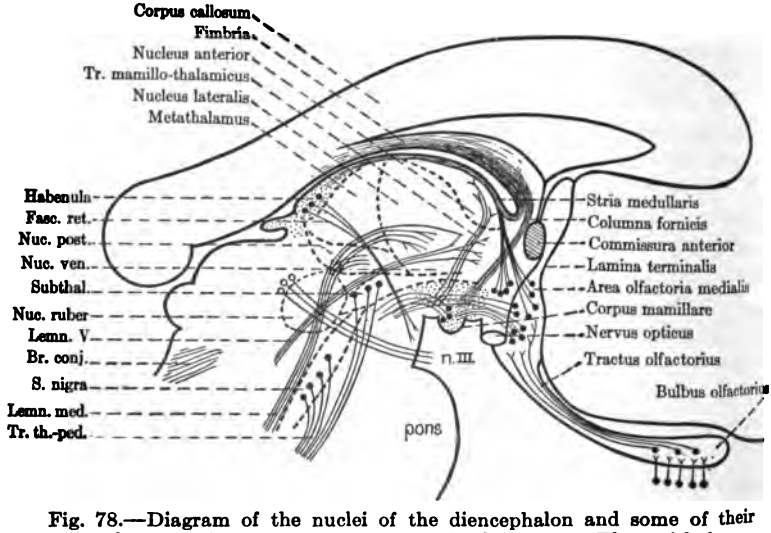

Fig. 78.—Diagram of the nuclei of the diencephalon and some of their functional connections as seen in parasagittal section. The epithalamus and the hypothalamus are stippled. *Br.conj.*, brachium conjunctivum; *Fasc.ret.*, fasciculus retroflexus; *Lemn. med.*, lemniscus medialis; *Lemn.V.*, lemniscus trigemini; *Nuc.post.*, nucleus posterior thalami; *Nuc.ven.*, nucleus ventralis thalami; *Subthal.*, subthalamus; *S.nigra*, substantia nigra; *Tr.th.-ped.*, tractus thalamo-peduncularis. This diagram should be studied in connection with a median section of the entire brain such as is shown in Figs. 51 and 52, p. 128, and Fig. 106, p. 246.

all pass through or near the internal capsule of the corpus striatum (p. 183 and Figs. 45, 79, 80). As we have just seen, the nuclei of the lateral group receive special systems of somatic

sensory fibers—optic, acoustic, and the general cutaneous and deep sensibility complex of the spinal, trigeminal, and medial lemnisci. The elements of the latter complex (comprising touch, temperature, pain, general proprioceptive sensibility, spatial localization, etc., termed as a whole the somesthetic group) are no doubt separately represented in the thalamus, but the analysis of their respective thalamic centers has not yet been completely effected. Each of the chief functional regions of the neothala-

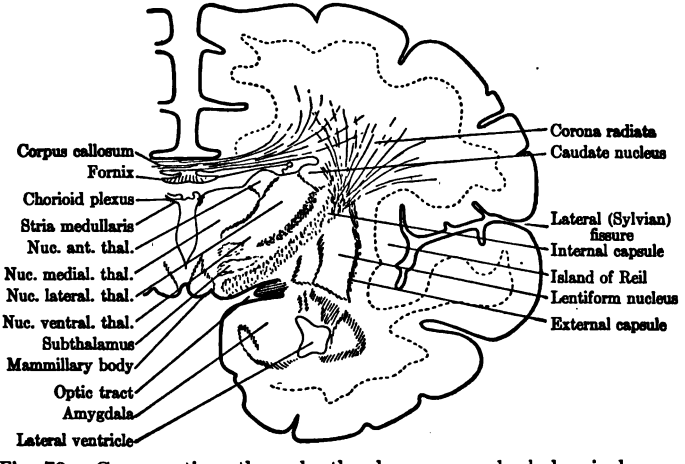

Fig. 79.—Cross-section through the human cerebral hemisphere and thalamus, including the mammillary body and the posterior end of the anterior nucleus of the thalamus (cf. Fig. 78). At this level the epithalamus is represented only by the stria medullaris and the chorioid plexus of the third ventricle, the hypothalamus by the mammillary body. The old thalamus (palæothalamus) is represented by the anterior and medial nuclei and the subthalamus, the new thalamus (neothalamus) by the lateral and ventral nuclei.

mus which have just been enumerated is connected by its own system of projection fibers with a specific region in the cerebral cortex, viz., the optic, auditory, and somesthetic projection centers (see p. 320). These tracts are known as the optic, auditory, and somesthetic radiations (see Fig. 80).

The old thalamus (palæothalamus) comprises the more medial thalamic centers which were differentiated for the primitive thalamic correlations which are present in fishes and

other lower vertebrates which lack the cerebral cortex (see Herrick, 1917). Clinical evidence (see especially Head and Holmes, 1911) seems to show that many of these primitive functions are retained in the old thalamus in man, and that some of the conscious activities are served by these thalamic centers. In other words, the activity of the cerebral cortex is not essential for all conscious processes, though its participation is necessary for others, particularly all intellectual and voluntary activities. The thalamus, on the other hand, can act independently of the cortex in the case of painful sensibility and the entire series of pleasurable and painful qualities; for the thalamic centers when isolated from their cortical connections are found to be concerned mainly with affective experience, and destructive lesions which involve the cortex alone do not disturb the painful and affective qualities of sensation (see p. 283).

The experiments of F. T. Rogers on decerebrate birds support the belief that the thalamus contains mechanisms for visceral adjustment which are lacking in the cerebral cortex. He concludes that in birds with the thalamus intact and the cerebral hemispheres removed the inhibitory effects of external stimuli (especially light and sound) upon visceral movements are lost, but that effects of visceral and painful stimuli are preserved. He shows, further, that the well-known restlessness of decerebrate birds (somatic movements of walking about, etc.) is not primarily excited by external (somatic sensory) stimuli, but by various types of visceral activity.

The relations of the thalamic nuclei and of some of the tracts connected with them are shown as seen from above in Fig. 77 and in a section parallel with the median plane in Fig. 78. Some of these centers are seen in cross-section in Fig. 79. The preceding analysis of the diencephalon, which differs in some respects from that of the B. N. A. (p. 129), is summarized in the accompanying table (p. 183), which includes also a few of the more important fiber tracts connected with each nucleus.

In front of the thalamus lie the corpus striatum and olfactory centers (see Figs. 45, 76, 78, 106), and above these last two is spread the great expanse of the cerebral cortex or pallium. The

THE DIENCEPHALON

I. Epithalamus.
  1. Membranous roof of the third ventricle.
  2. Pineal body (epiphysis).
  3. Habenula (receives the stria medullaris from the olfactory centers and sends fibers to the cerebral peduncle).

II. Thalamus.
  1. Dorsal part.
    (1) Medial group of nuclei.
      (*a*) Medial nucleus (receives fibers from the olfactory area and neothalamus and from the trigeminal lemniscus; sends fibers to the olfactory area, corpus striatum, subthalamus, and probably cerebral cortex).
      (*b*) Anterior (or dorsal) nucleus (receives fibers from the mammillary body and sends fibers to the corpus striatum).
    (2) Lateral group of nuclei (neothalamus).
      (*a*) Lateral, ventral, and posterior nuclei (receive the medial, spinal, and trigeminal lemnisci; connect with parietal and frontal cortex by ascending and descending somesthetic projection fibers).
      (*b*) Pulvinar and lateral geniculate body (receive optic tracts; connect with occipital cortex by ascending and descending optic projection fibers).
      (*c*) Medial geniculate body (receives the lateral or acoustic lemniscus; connects with temporal cortex by ascending and descending auditory projection fibers).

    [The two geniculate bodies = metathalamus, B. N. A.]
  2. Ventral part, or subthalamus (a motor coördination center receiving fibers from the dorsal part of the thalamus, from the corpus striatum and from the pyramidal tract; sends fibers to the pedunculus cerebri; comprises the body of Luys, Forel's field H_2, and some adjacent gray matter; is continuous behind with the substantia nigra of the cerebral peduncle).

III Hypothalamus.
  1. Tuber cinereum (olfacto-visceral correlation center).
  2. Mammillary body (receives fibers from the olfactory centers; sends fibers to the cerebral peduncle and nucleus anterior thalami).
  3. Hypophysis.

corpus striatum consists of masses of gray matter separated by sheets of white matter, an arrangement which gives a striated appearance in section.

In studying the comparative anatomy of the cerebral hemispheres we find the corpus striatum well developed in some

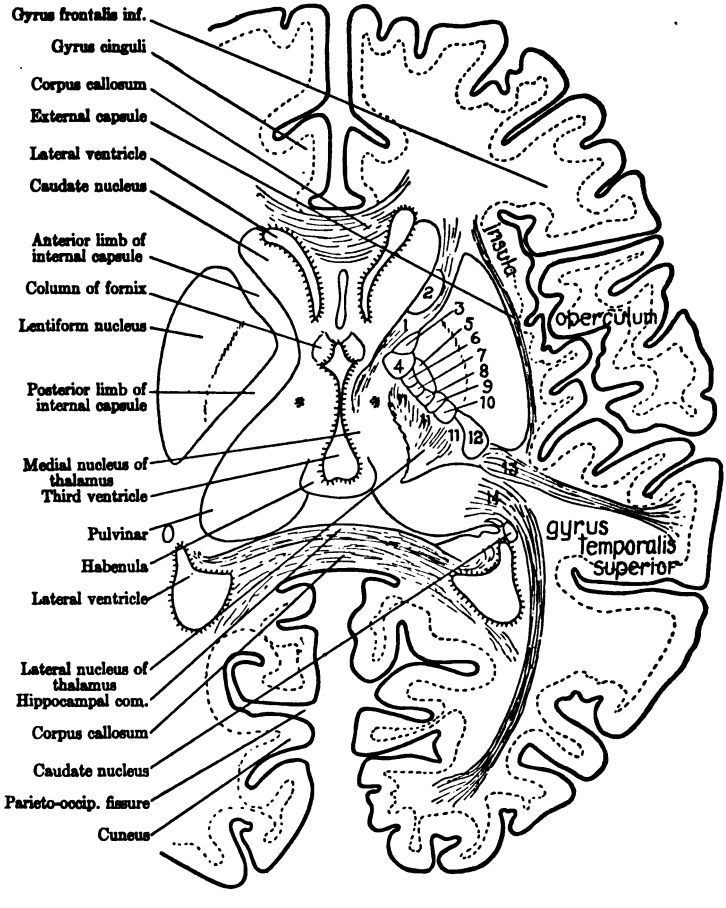

Fig. 80.—Longitudinal section through the human cerebral hemisphere passing through the internal capsule, some of the fiber systems of which are numbered as listed below:

1. Frontal thalamic tracts between the medial nucleus of the thalamus and the frontal lobe of the cerebral cortex.
2. Frontal pontile tract between the frontal lobe of the cortex and the pons.
3. Cortico-oculomotor tract from the motor cortex to the nucleus of the oculomotor nerve.
4. Cortico-bulbar tracts from the motor cortex to the motor nuclei of the medulla oblongata.

lower vertebrates which lack the cerebral cortex, and very highly developed in others, like reptiles and birds, where the cortex is present, though very small. In these animals the corpus striatum appears to be a reflex center of great importance and of higher order than the thalamus; and the differentiation of this apparatus seems to have been a necessary precursor of the elaboration of the cerebral cortex as we find it in the mammals.

The gray matter of the mammalian corpus striatum is arranged in two principal masses, the caudate nucleus (Figs. 45, 76) and the lentiform nucleus (Figs. 79, 80), and the latter is divided by a band of white fibers into a lateral putamen and a medial globus pallidus. The caudate nucleus receives fibers from the anterior and medial nuclei of the thalamus (old thalamus) and is broadly connected with the putamen. Both of these nuclei send their nervous impulses into the globus pallidus, which is chiefly an efferent center discharging into the ventral part of the thalamus, hypothalamus, and cerebral peduncle (Wilson, 1914). The globus pallidus contains chiefly large cells of the motor type, some of which are also scattered through other parts of the striatum. The corpus striatum seems to be a control center for fundamental motor reflexes whose efferent fibers arise from the large cells of the globus pallidus type. Hunt (1917) believes that the caudate nucleus and putamen exert a regulatory and inhibiting influence upon the strictly

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5. Cortico-rubral tract from the motor cortex to the nucleus ruber.

6 to 10. Pyramidal tract (tractus cortico-spinalis) from the motor cortex to the spinal cord, with the following parts—

6. To the cervical spinal cord for the muscles of the shoulder.
7. To the cervical cord for the muscles of the arm.
8. To the cervical cord for the muscles of the hand.
9. To the lumbar cord for the muscles of the leg.
10. To the lumbar cord for the muscles of the foot.

11. Somesthetic radiations from the lateral and ventral nuclei of the thalamus to the cerebral cortex.

12. Occipito-temporal pontile tract to the pons, and temporo-thalamic tract to the thalamus.

13. Auditory radiation from the medial geniculate body to the superior temporal gyrus.

14. Optic radiation from the pulvinar and lateral geniculate body to the cuneus in the occipital lobe of the cortex.

motor functions of the globus pallidus. Injury to the two former is said to be characterized chiefly by tremor and twitching of the muscles (Wilson, 1912), that of the globus pallidus chiefly by rigidity and tremor.

Ramón y Cajal is of the opinion that the mammalian striatum functions also to reinforce the descending motor impulses which leave the cerebral cortex, these systems of fibers giving off collateral branches as they traverse it.

The white matter of the corpus striatum consists partly of the fibers already mentioned as passing between it and the thalamus and cortex, but chiefly of fibers passing between the cortex and deeper parts of the brain stem, having no functional connection with the striatum itself. These are called projection fibers. They are partly ascending and descending fibers passing between the thalamus and the cortex (the optic, auditory, and somesthetic projection systems, or radiations, which have already been mentioned, p. 180), and partly descending motor projection fibers of the cortico-spinal or pyramidal tract (p. 151 and Fig. 64, p. 152), cortico-bulbar tract, and cortico-pontile tracts (pp. 207 and 317).

Most of the projection fibers pass between the lentiform nucleus laterally and the caudate nucleus and thalamus medially in a wide band of white matter known as the internal capsule. These fibers are exposed in the dissection shown in Fig. 45. As these fibers radiate from the internal capsule toward the cortex they are called the corona radiata (Fig. 79). The external capsule is a thinner sheet of fibers externally of the lentiform nucleus (Figs. 79 and 80). Figure 79 illustrates a transverse section through the cerebral hemisphere, showing the relations of the thalamus and corpus striatum.

The exact arrangement of the functional systems of sensory and motor projection fibers within the internal capsule is a matter of great clinical importance; for a considerable proportion of apoplexies and other cerebral diseases result from hemorrhage or other injury of the internal capsule causing destruction of some of its fibers. A partial paralysis will result, whose symptoms will depend upon the particular functional systems of projection fibers affected. Figure 80 illustrates the arrangement of some of the systems of fibers of the internal

capsule as seen in a horizontal section through the cerebral hemispheres. For more detailed discussion see the works of Déjerine and Tilney and Riley cited on page 14.

The olfactory centers of the cerebral hemispheres and the cerebral cortex will be considered in chapters which follow.

Summary.—The cerebrum contains the primary centers for the I, II, III, and IV pairs of cranial nerves, but most of its substance is concerned with the higher centers for the correlation of sensory impressions, especially those involved in the psychic activities. The midbrain contains in the corpora quadrigemina important reflex correlation centers of sight and hearing, and in the cerebral peduncle centers for the coördination of movements. The diencephalon is devoted chiefly to various types of correlation. It is divided into three parts, the thalamus, the epithalamus, and the hypothalamus, the two last being dominated by the olfactory system. The thalamus contains a medial group of nuclei concerned with thalamic reflexes and the affective experience and a lateral group of nuclei which discharge the sensory projection fibers of sight, hearing, and general sensibility into the cerebral cortex. The subdivision of the diencephalon is summarized in the table on p. 183. The corpus striatum in lower vertebrates is an important reflex center; in man its functions seem to be subsidiary to those of the cerebral cortex for the most part. It consists of two chief masses of gray matter, the caudate and lentiform nuclei, with sheets of white matter between and within these masses. The chief systems of fibers of the white matter are accumulated in the internal capsule which lies between the lentiform nucleus laterally and the caudate nucleus and thalamus medially. Through the internal capsule run the projection fibers which connect the cerebral cortex with the lower parts of the brain stem, including the sensory radiations from the thalamus and the descending systems to the pons and brain stem and the great pyramidal tract, which is the voluntary motor path from the cortex to the spinal cord.

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CHAPTER XI

THE GENERAL SOMATIC SYSTEMS OF CONDUCTION PATHS

In this and the following chapters we shall review the conduction pathways followed by some of the chief sensori-motor systems and add some further details to the general description already given, beginning with the more generalized somatic sensory functions.

Clinical neurologists have long been in the habit of grouping together the different forms of deep and cutaneous sensibility under the term "general sensibility." The more refined researches of recent students (especially Sherrington, Head, Trotter and Davies, Brouwer, Boring, see the bibliographies on pp. 100 and 153) have given us a much more precise analysis of these systems, as already explained. The peripheral nerves of deep sensibility (exclusive of those devoted to strictly visceral functions) are anatomically distinct from those of cutaneous sensibility. Physiologically, the nerves of deep sensibility are devoted chiefly to proprioceptive functions (muscle sensibility, joint sensibility, etc.), and the nerves of cutaneous sensibility chiefly to exteroceptive functions (touch, temperature, and pain); but this holds only approximately, for nerves of deep sensibility may also serve the exteroceptive functions of pressure and painful response to overstimulation, though with a higher stimulus threshold than in the skin, and the cutaneous nerves also participate to some extent in the proprioceptive functions of spatial orientation of the body and its members (see pp. 82 ff. and 142).

Exteroceptive Systems.—The nerves serving the functions of touch, pressure, temperature, and pain of the body and limbs, whether derived from the skin or the deep tissues, soon after their entrance into the spinal cord terminate in the gray matter of the dorsal column of the same side. After

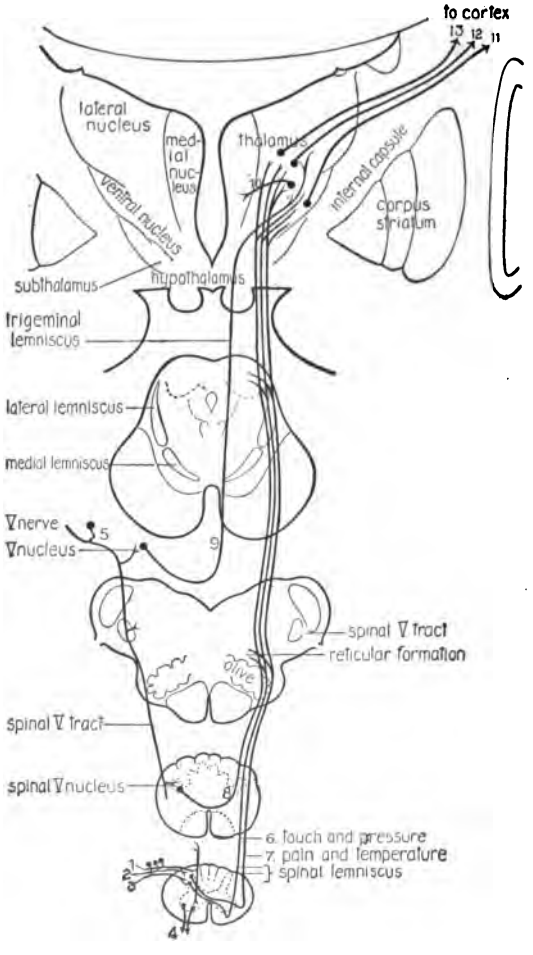

Fig. 81.—Diagram of the exteroceptive conduction pathways contained within the spinal cord and brain stem. The figure illustrates cross-sections of the central nervous system in the lower cervical region of the spinal cord, at the level where the cord passes over into the medulla oblongata, at the level of the roots of the VIII cranial nerve, through the inferior colliculus and through the thalamus.

1. Connections of peripheral neuron of touch, temperature, or pain for intrinsic spinal reflexes.

2. Peripheral neuron of pain or temperature.

a synapse here the axons of the neurons of the second order cross to the opposite side of the cord and ascend in the spinal lemniscus to the thalamus. For further details of these connections see pages 150, 151, 178–182, and Figs. 59, 63, 64, 75, 77, 80, 81; on the pain path, see also p. 281. The pathway for cutaneous sensibility from the head follows the trigeminal lemniscus (pp. 171, 197. and Figs. 64, 75, 77, 78, 81). The more important exteroceptive pathways are assembled in Fig. 81.

It will be recalled that in the spinal lemniscus the pathways for touch and pressure, for pain and for temperature are assembled in three distinct tracts, those for pain and temperature being close together (Fig. 63, p. 149). From this it follows that small circumscribed injuries in the white substance of the spinal cord may destroy all sensibility to pressure in a part of the body without any considerable disturbance of pain or temperature sensibility, or conversely, it may destroy pain or temperature sensibility without any involvement of the other qualities of sensation. And, in fact, in numerous clinical cases these conditions are found, as will be clear from the following example.

Figure 82 illustrates such a case from Dr. Head's experience. The patient suffered from an injury to the lower part of the spinal cord caused by the overturning of a truck of concrete, and when admitted to the London Hospital was paralyzed from the hips downward. In the course of a year he partly recovered, but showed a permanent loss of some sensation qualities over the shaded area in the figure. The right leg below the knee was insensitive to pain (prick) and to all degrees of temperature. But over the whole of this area he

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3. Peripheral neuron of touch and pressure.
4. Peripheral motor neurons of spinal nerve.
5. Peripheral cutaneous neuron of trigeminal nerve.
6. Secondary neuron of touch and pressure in spinal lemniscus.
7. Secondary neuron of pain or temperature in spinal lemniscus.
8. Secondary neuron from lower part of spinal V nucleus entering the spinal lemniscus.
9. Secondary neuron from chief sensory V nucleus entering the trigeminal lemniscus.
10. Intrinsic correlation neuron of thalamus for thalamic reflexes.
11, 12, 13. Thalamo-cortical radiations to the postcentral gyrus.

could appreciate all tactile stimuli and could localize accurately the spot touched or pressed upon. Yet it was not possible to produce pain anywhere over the right leg and foot by excessive pressure, although he fully recognized its gradual increase. Referring to Fig. 63 (p. 149), it is evident that to produce these symptoms the lesion must have involved the conduction path for pain and temperature in the lateral funiculus (fiber 8 of the figure) of the left side of the spinal

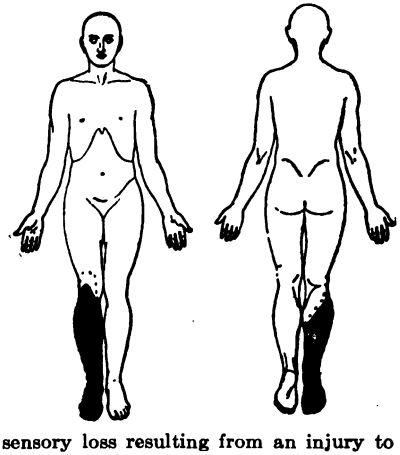

Fig. 82.—The sensory loss resulting from an injury to the lower part of the spinal cord. The shaded area represents the parts insensitive to cutaneous painful stimuli and also to the pain of excessive pressure; yet over this area light touch and the tactile element of pressure were appreciated. (After Head and Thompson.)

cord, and spared the path for touch and pressure in the ventral funiculus (fiber 9). Both superficial pain (prick) and deep pain caused by excessive pressure were abolished. This combination of symptoms could not be produced by any injury to the nerve-roots or peripheral branches. For other cases, see Spiller (1915).

Proprioceptive Systems.—Referring back to p. 149, we are reminded that the ascending proprioceptive fibers of the spinal cord effect three types of connections within the brain: (1) in the cerebellum; (2) in the brain stem; (3) in the cerebral cortex. The connections of the second and third types are made

through the dorsal funiculus and medial lemniscus; they are shown in Figs. 59, 63, 64, 75, 77, 78, 80, and 84, and in a more comprehensive way in Fig. 83.

The cortical proprioceptive pathway in its simplest form may consist of a chain of only three neurons: (1) A peripheral neuron whose cell body lies in some spinal ganglion, whose dendrite reaches some organ of muscle sense, tendon sense, or similar receptor, and whose axon terminates at the upper end of the cord in the nucleus of the fasciculus gracilis or fasciculus cuneatus of the same side; (2) the body of the second neuron lies in one of the nuclei last mentioned (marked nucleus of dorsal funiculus in Fig. 64), its axon ascends in the medial lemniscus, and terminates in the lateral and ventral nuclei of the thalamus of the opposite side (Figs. 77 and 83); (3) the neuron of the third order lies in the thalamus and sends its axon through the internal capsule to the somesthetic area of the cerebral cortex.

The dorsal funiculi of the spinal cord have until recently been regarded as the chief ascending pathway for all forms of sensibility, and much of the clinical practice now in vogue is based upon this assumption. But evidently such an assumption is untenable. The dorsal funiculi seem to be concerned chiefly with the proprioceptive group of reactions. These may be unconscious reflexes of motor coördination and the maintenance of equilibrium, or they may come into consciousness as sensations of position and orientation of the body and its parts and of spatial discrimination. Purely exteroceptive stimuli, whether transmitted by the deep nerves or by the cutaneous nerves, may be carried for a few segments in the dorsal funiculi (Fig. 81, neuron 1); but they are soon filtered off into the gray matter of the dorsal column, and after a synapse here they are sorted into functionally distinct tracts on the opposite side of the cord. The tactile elements of the mixed peripheral root fibers entering the dorsal funiculus are drawn off later than are the elements for thermal and painful sensibility; and some of the components commonly reckoned with cutaneous exteroceptive sensibility remain in the dorsal funiculus for its entire length. These are chiefly two-point discrimination, and discrimination of size, shape, form, and

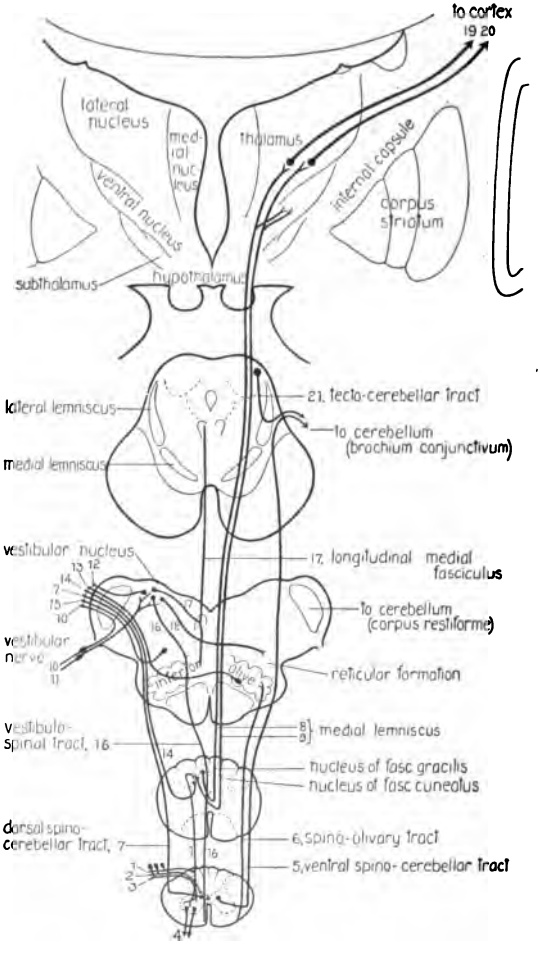

Fig. 83.—Diagram of the chief proprioceptive conduction pathways contained within the spinal cord and brain stem. The mesencephalic root of the trigeminal nerve (see p. 197 and Figs. 71 and 77) is omitted and not all of the cerebellar connections are indicated. The connection to the cerebellum from the nuclei of the fasciculi gracilis and cuneatus (neuron 14) is controverted, but it is well established that similar connections are effected immediately below this level from the dorsal funiculus of the cord. The figure illustrates cross-sections of the central nervous system in the lower cervical region of the spinal cord, at the level where the cord passes over

texture of surfaces. These all involve a comparison and discrimination in consciousness of spatial factors and are, therefore, bound up with those fibers which serve the proprioceptive reflexes, which are unconscious spatial adjustments.

Some peculiar combinations of symptoms arise from the fact that, whereas the ascending proprioceptive impulses (so far as these are consciously perceived) pass up in the dorsal funiculus of the *same* side for the entire length of the cord, the impulses of the exteroceptive impulses, within a few segments of their point of entrance into the cord, are transferred to the *opposite* side to ascend in the spinal lemniscus tracts. From this it follows that a localized central injury involving the dorsal gray column and dorsal funiculus of one side only will cut off all ascending proprioceptive impulses which pass through the dorsal funiculus from lower levels on the same side of the body as the lesion, and at the same time will abolish both proprioceptive and exteroceptive functions in a circumscribed region of the same side of the body whose exteroceptive neurons of the first order discharge into the injured part of the dorsal gray column.

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into the medulla oblongata, at the level of the roots of the VIII cranial nerve, through the inferior colliculus, and through the thalamus.

1. Peripheral neuron entering the dorsal funiculus and also effecting intrinsic spinal reflex connections.
2. Peripheral neuron entering the nucleus dorsalis of Clarke.
3. Peripheral neuron effecting connections with the intrinsic correlation neurons of the spinal cord.
4. Peripheral motor neurons of spinal nerve.
5. Ventral spino-cerebellar tract.
6. Spino-olivary tract.
7. Dorsal spino-cerebellar tract.
8, 9. Medial lemniscus.
10. Vestibular root fiber passing directly into the cerebellum.
11. Vestibular root fiber entering the vestibular nucleus.
12. Vestibulo-cerebellar tract.
13. Olivo-cerebellar-tract.
14. Path from the dorsal funiculus (or its nuclei) to the cerebellum.
15. Path from the reticular formation to the cerebellum.
16. Vestibulo-spinal tract.
17. Path from the vestibular nucleus to the fasciculus longitudinalis medialis.
18. Path from the vestibular nucleus to the reticular formation.
19, 20. Thalamic radiations to the cerebral cortex.
21. Tecto-cerebellar tract.

Head and Thompson (1906) describe a case involving the loss of sensibility to painful stimuli in the left neck, arm, and upper thorax resulting from a tumor in the cervical region of the spinal cord. Tactile, temperature, and deep sensibility were also profoundly disturbed over approximately the same region (the temperature disturbance involving the right side also). These symptoms resulted from the destruction of all dorsal root fibers in the affected area at the point of their entrance into the cord or of the gray substance containing the terminals of these fibers, a purely local effect. That the dorsal funiculus of the same side was also involved is shown by symptoms of remote effects of the injury in the left foot. Strictly exteroceptive sensibility (touch, temperature, pain) was preserved in both legs, but the left leg was devoid of proprioceptive sensibility, as shown by the loss of ability to appreciate the passive position or movement of the leg and failure to discriminate two points with the compass test.

The intrinsic connections within the cord for spinal reflexes are undoubtedly very primitive. These are both exteroceptive and proprioceptive in type (p. 143). We have seen that the ascending tracts between the spinal cord and the brain fall into two groups: (1) The exteroceptive systems in the spinal lemniscus, and (2) the proprioceptive systems in the dorsal funiculus and medial lemniscus. Comparative anatomy shows that the spinal lemniscus system is much older phylogenetically than the medial lemniscus system. The fishes possess well-defined spino-tectal and spino-thalamic tracts, but their dorsal funiculus possesses only the fasciculus proprius fibers (cf. Figs. 66, 67, pp. 164, 165) and they lack the medial lemniscus altogether. The spinocerebellar tracts, on the other hand, are very ancient and are present from the lowest to the highest vertebrates.

These considerations suggest that the first fibers to pass from the spinal cord to the higher centers of the brain, and presumably the first sensory impulses from the spinal nerves to be consciously perceived, were those of touch and temperature transmitted through the spinal lemniscus. (Pain is probably also very primitive as a conscious experience, but it is doubtful whether it is represented in the spinal lemniscus of lower forms; see p. 281). The proprioceptive impulses in lower vertebrates are coördinated quite unconsciously in the brain stem and cerebellum, and it is only in the higher forms that this system of nervous impulses reaches the thalamus (through the medial lemniscus) and cerebral cortex for conscious control. Clinical evidence shows that the medial lemniscus connections in man are concerned with the conscious adjustments of the positions and orientation in space of the body and its members and with spatial discriminations of various sorts, rather than with the senses of touch and pressure as externally projected.

The innervation of the organs of muscular sensibility and tendon sen-

sibility in the head is not as fully known as in the case of those of the trunk and limbs, as above described. Sherrington and Tozer have recently shown that such organs are present in the muscles which move the eyeball and that their nerves accompany the motor fibers of the III, IV, and VI cranial nerves; but of the central connections of these sensory nerve-fibers of the eye muscles nothing is known. It is suggested by the researches of Johnston, Willems, Allen, and others that the jaw muscles, which receive their motor innervation from the motor V nucleus (nucleus masticatorius), receive their sensory innervation from the mesencephalic nucleus of the V nerve, whose position along the lateral border of the aqueduct of Sylvius is seen in Figs. 71, 75, and 77. But recent studies of Edgeworth have shown that these muscles also receive sensory fibers from the semilunar or Gasserian ganglion of the V nerve, and the question requires further investigation. After removal of the Gasserian ganglion pressure-pain may persist in the face and tongue. It is suggested by Maloney and Kennedy (1911) that the head sympathetic subserves a general crude sensibility to pressure-pain of the protopathic type with high threshold which may persist after removal of the Gasserian ganglion.

The fibers of the chief sensory root of the V nerve in part end in the chief sensory V nucleus near the level of their entrance into the medulla oblongata (Figs. 71, 77) and in part pass downward through the whole length of the medulla oblongata and upper levels of the spinal cord as the spinal V tract (Figs. 64, 71, 72, 81). It has been suggested by comparative evidence that the spinal V tract and its nucleus are connected with a phylogenetically old type of reaction to touch, temperature, and pain, probably chiefly reflex, while the chief nucleus is concerned with the more recently acquired discriminations of these systems with more direct cortical connections. Some clinical and pathological evidence, on the other hand, suggests that the chief nucleus receives fibers of tactile sensibility and the spinal nucleus the fibers of temperature and painful sensibility (Spiller, 1915). The fibers of the secondary tract, or trigeminal lemniscus (p. 171), follow two separate paths, a dorsal and a ventral, both of which are shown in Fig. 81 (fibers 9 and 8 respectively), but only the dorsal in Figs. 75 and 77 (in Fig. 75 this is drawn too far ventral, its true position is near the tractus thalamo-olivaris). The fibers of the ventral tract are crossed, those of the dorsal tract are partly uncrossed. The fibers of the trigeminal lemniscus which mediate cutaneous sensibility of the head terminate farther forward in the thalamus than do the fibers of the spinal lemniscus systems which mediate cutaneous sensibility of the trunk and limbs.

Motor Paths.—Throughout the length of the spinal cord and brain stem the ascending fibers of both exteroceptive and proprioceptive sensibility give off collateral branches into the reticular formation (p. 172) for reflex connections with the motor nuclei at various levels. The arrangement of these motor nuclei of the brain stem, from which peripheral motor fibers of the cranial nerves arise, is shown on the left side of Fig. 71 (p. 168). The details of these connections for local motor reflexes will not be entered into here. From the ventral

part of the thalamus (p. 179) there are descending thalamo-bulbar and thalamo-spinal tracts for local thalamic reflexes, and from the corpus striatum there is a descending system of motor fibers which seems to exert a tonic and steadying influence upon voluntary movement (p. 185). The main descending

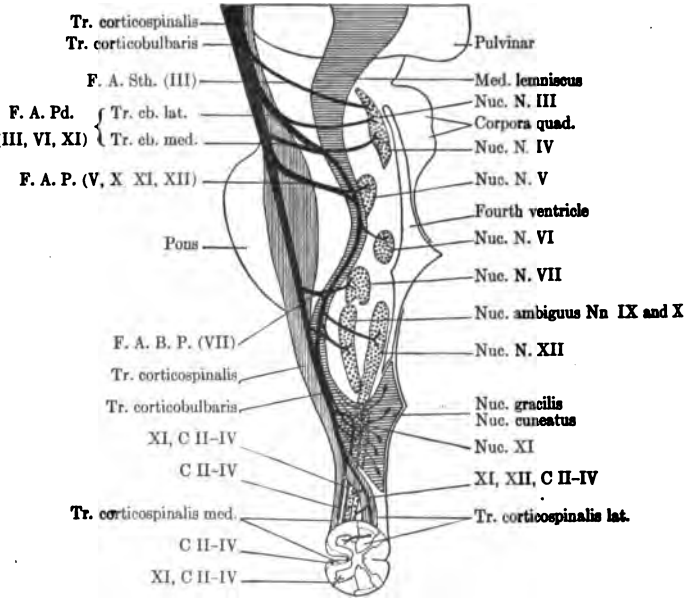

Fig. 84.—The course of the fibers of the cortico-bulbar tract. (Dejerine, Ranson.) Cortico-bulbar tract, solid black; cortico-spinal tract, vertical lines; medial lemniscus, horizontal lines; *F. A. B. P.*, bulbopontine aberrant fibers; *F. A. P.*, pontine aberrant fibers; *F. A. Pd.*, peduncular aberrant fibers; *F. A. Sth.*, subthalamic aberrant fibers; *Tr. cb. lat.*, tractus cortico-bulbaris lateralis; *Tr. cb. med.*, tractus cortico-bulbaris medialis. The Roman numerals indicate the nuclei of the cranial and cervical nerves which are supplied by the various bundles.

pathway for voluntary motor responses to general somatic stimuli arises from the precentral gyrus of the cerebral cortex (p. 317). This is the tractus cortico-spinalis, or pyramidal tract (p. 319 and Figs. 64, 72 to 75, and 140) and the associated

cortico-bulbar tract (Figs. 75, 80 (3 and 4)). The latter fibers accompany the pyramidal tract for part of their course and in the brain stem are detached in small fascicles (the so-called aberrant pyramidal fibers) to reach the appropriate nuclei of the cranial nerves, as illustrated in Fig. 84. The reflex connections effected in the medulla oblongata are somewhat more complex than those of the spinal cord, that is, they represent the integration of more different kinds of sensory impulses and facilitate the performance of a greater variety of movements by way of response. Similarly, the complexity of the reflex adjustments increases as we pass forward into the midbrain, thalamus, and cerebral cortex (see p. 122).

Attention has already been called to the fact that the centers of adjustment in the brain stem are of two physiologically different types which we have termed centers of correlation and centers of coördination (p. 36). The more labile and individually variable adjustments are effected in the correlation centers which are developed from the more dorsal parts of the embryonic neural tube above the limiting sulcus (p. 125), while the more ventral parts of the neural tube give rise to the motor centers and the centers of coördination, whose adjustments are of a more fixed and invariable character. In the embryonic development the coördination centers develop precociously, while the correlation centers mature more slowly; the higher association centers of the thalamus and cerebral cortex in particular are the last to mature (p. 322).

In the phylogenetic development of the brain the same rule holds. In the lowest vertebrates the coördination centers are much larger in proportion to the size of the correlation centers than in higher vertebrates. Bartelmez has analyzed these motor coördination mechanisms (which he terms in the aggregate the nucleus motorius tegmenti) in fishes, and finds in the motor tegmentum throughout the medulla oblongata a nucleus of a primitive type whose neurons serve to connect the primary sensory nuclei with the primary motor nuclei. Some of these connections are very short, while others are very long, reaching remote parts of the brain and spinal cord through the longitudinal medial fasciculus (pp. 204, 237). This nucleus is the parent tissue out of which the more complex coördination centers in the tegmentum of higher vertebrates have been differentiated.

In very young amphibian embryos Coghill finds a still simpler condition which is probably also more primitive. In the spinal cords of these larvæ the individual neurons of the motor tegmentum give rise both to fibers of the longitudinal conduction tract of motor coördination (fasciculus proprius ventralis) and to peripheral fibers of the ventral roots, the latter arising as collaterals of the longitudinal axons. In older larvæ separate neurons have been differentiated for these two functions of peripheral conduction and longitudinal conduction. The steps in the embryologic development and probable evolution of the more complex centers of adjustment have been briefly reviewed by Herrick and Coghill (see pp. 71, 122).

Summary.—The old clinical concept "general sensibility" has recently been analyzed into a number of components, the most fundamental division being the distinction between a group of exteroceptive and a group of proprioceptive systems. The exteroceptive systems are transmitted from the spinal cord to the brain through a complex tract, the spinal lemniscus, within which there are separate pathways for the three qualities of sensation, touch, temperature, and pain. These sensation qualities come into consciousness with a distinct peripheral or external reference. The proprioceptive systems (muscle sense and allied types) are transmitted to the brain through the dorsal funiculus of the same side of the cord, the medial lemniscus of the opposite side, the thalamus, and the somesthetic radiations to the cerebral cortex; and also through the spino-cerebellar tracts to the cerebellar cortex. Most of these reactions of spatial adjustment do not come into consciousness at all, but some appear subjectively as sensations of posture, bodily movement, and spatial discrimination. The cerebellum is the great clearing house for these and all other afferent systems which are concerned in the proprioceptive functions, so far as these are unconsciously performed.

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CHAPTER XII

THE VESTIBULAR APPARATUS AND CEREBELLUM

THE general somatic sensory systems considered in the last chapter include some of the most primitive reflex mechanisms. These fall into two groups—the exteroceptive systems and the proprioceptive systems (pp. 82–93)—and each of these groups comprises, in addition to its primitive generalized members, certain so-called organs of special or higher sense. The special exteroceptive sense organs are the organ of hearing (p. 219) and the organ of vision (p. 230). The special proprioceptive sense organs are the semicircular canals of the internal ear; and those will next be described, together with their central mechanisms in the medulla oblongata and cerebellum.

The Vestibular Apparatus.—The internal ear contains two quite distinct groups of sense organs, the organ of hearing in the cochlea and the vestibular organs (utricle, saccule, and semicircular canals), both of which are supplied by the VIII cranial nerve, which accordingly has two parts, the cochlear and the vestibular nerves. The semicircular canals are the most highly specialized end-organs of the proprioceptive series and are concerned chiefly with the maintenance of bodily equilibrium. The general structure of the internal ear is described on p. 219; here we need merely mention that the three semicircular canals (ductus semicirculares) of each ear lie approximately at right angles to each other, as shown diagrammatically in Fig. 85, and each canal is dilated at one end to form the ampulla, within which is a patch of sensory epithelium from which hairs project into the contained fluid (see Figs. 32 and 91). A movement of the head in any direction will cause stimulation of the sensory cells in one or more of these canals in each ear, which in turn will excite a nervous impulse in the nerve supplying the corresponding ampullæ. These nervous impulses will be transmitted to the vestibular centers of the

brain, where they will be so analyzed as to call forth the appropriate reaction to the movement which has excited the particular semicircular canals involved.

The fibers of the vestibular nerve enter the medulla oblongata immediately behind the pons and terminate in a vestibular nucleus which forms an eminence on the floor of the fourth

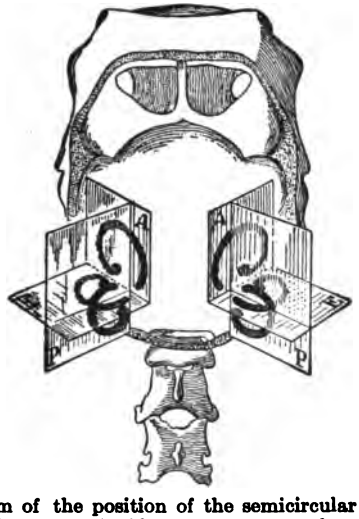

Fig. 85.—Diagram of the position of the semicircular canals in the head, as seen from behind. On each side it will be seen that the three canals lie in planes at right angles to one another. The external or horizontal canals (*E*) of the two sides lie in the same plane. The anterior canal of one side (*A*) lies in a plane parallel to that of the posterior canal (*P*) of the other side. (After Ewald.)

ventricle in this region (Figs. 71, 96). This nucleus has four subdivisions, as follows:

Nucleus nervi vestibuli medialis (of Schwalbe, also called nucleus dorsalis, triangular nucleus and principal nucleus).
Nucleus nervi vestibuli lateralis (of Deiters, also called nucleus magnocellularis).
Nucleus nervi vestibuli superior (of Bechterew).
Nucleus nervi vestibuli spinalis.

The arrangement of these nuclei and of some of their secondary connections is shown in Fig. 86. Some of these connections are made with the motor nuclei and reticular formation of the

medulla oblongata for local bulbar reflexes; there is a vestibulo-spinal tract (*tr.v.sp.*) for movements of the trunk and limbs

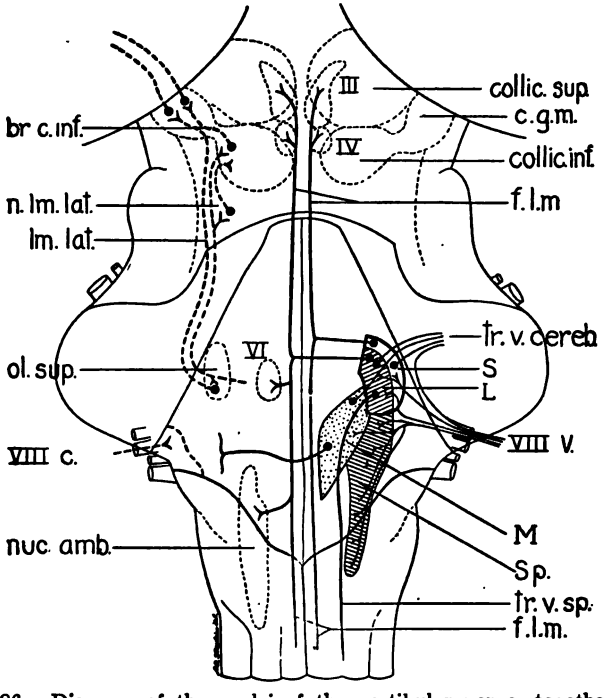

Fig. 86.—Diagram of the nuclei of the vestibular nerve, together with some of the associated fiber tracts. The secondary tracts associated with the vestibular nuclei are drawn in full lines; a part of the secondary auditory path from the cochlear nuclei is drawn in broken lines. Compare Figs. 71, 77, 96. *br.c.inf.*, brachium quadrigeminum inferius; *c.g.m.*, corpus geniculatum mediale; *collic. inf.*, colliculus inferior; *collic. sup.*, colliculus superior; *f.l.m.*, fasciculus longitudinalis medialis; *L*, nucleus nervi vestibuli lateralis (Deiters); *lm. lat.*, lemniscus lateralis; *M*, nucleus nervi vestibuli medialis (Schwalbe); *n.lm. lat.*, nucleus of lemniscus lateralis; *nuc. amb.*, nucleus ambiguus; *ol. sup.*, superior olive; *S*, nucleus nervi vestibuli superior (Bechterew); *Sp.*, nucleus spinalis nervi vestibuli; *tr. v. cereb.*, tractus vestibulocerebellaris; *tr.v.sp.*, tractus vestibulo-spinalis; *VIII c.*, radix cochlearis of VIII nerve; *VIII v.*, radix vestibularis of VIII nerve. For a more accurate reconstruction of these nuclei see Weed (Pub. of the Carnegie Inst. of Washington, No. 191, 1914).

in response to stimulation of the semicircular canals; and there is also a strong connection with the longitudinal medial fascicu-

lus (*f.l.m.*), by which fibers descend to the spinal cord (chiefly for turning movements of the head by the neck muscles) and ascend to the midbrain. The last-mentioned fibers connect chiefly with the nuclei of the motor nerves for the eye muscles (III, IV, and VI pairs of cranial nerves), thus providing for the conjugate movements of the eyes which accompany head movements (in this way, for instance, enabling one to keep the gaze fixed upon a stationary object while the head is moving, cf. p. 237).

It will be noticed that there is no important pathway from the vestibular nucleus to the thalamus and cerebral cortex, for the equilibratory reactions excited from the semicircular canals are normally unconsciously performed. This is in marked contrast with the connections of the cochlear nerve, for the auditory reactions are often consciously directed (p. 224). There is, however, an important connection with the cerebellum, partly directly by root fibers of the vestibular nerve and partly by secondary fibers from the superior and lateral vestibular nuclei (Fig. 86). The cerebellum is, accordingly, an important center of adjustment for the proprioceptive reflexes, and to this our attention will next be directed.

The Cerebellum.—This important organ is an overlord which dominates the proprioceptive functions of the body in somewhat the same way that the cerebral cortex directs and controls the exteroceptive reactions. Both of these organs are secondarily added to the more primitive segmental structures of the brain stem, that is, they are suprasegmental (p. 122).

The correlation centers of the brain stem, and particularly those of the cerebral cortex, analyze the afferent impulses entering the brain and determine what particular reactions are appropriate in each situation. After the character of the movement has been determined in this way, the proprioceptive systems coöperate in its execution, and the cerebellum is the central coördination station for the proprioceptive reactions. None of its activities come into consciousness.

The cerebellum, therefore, is intimately connected with all sensory centers which are concerned in the adjustment of the body in space and motor control in general. The maintenance of muscular tone and of bodily equilibrium are the most

important of these functions, and the semicircular canals of the internal ear (pp. 93, 220) are the receptive organs which

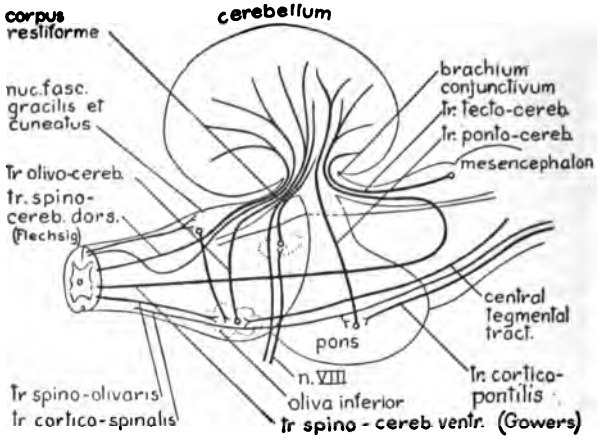

Fig. 87, *A*.—Diagram of the chief afferent tracts leading into the cerebellum.

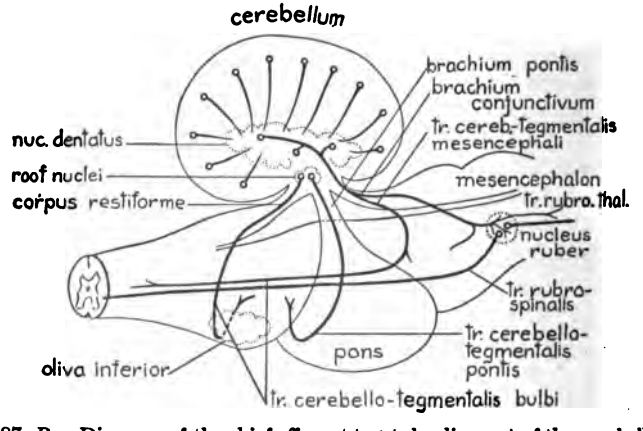

Fig. 87, *B*.—Diagram of the chief efferent tracts leading out of the cerebellum.

are of chief importance in these reactions. Comparative and embryological studies show that the cerebellum was developed

as a direct outgrowth from the primary centers for the semicircular canals in the medulla oblongata (the acoustico-lateral area of fishes, Figs. 43, 68A, cf. Herrick, 1914), and even in the human body root fibers from the vestibular branch of the VIII cranial nerve enter the cerebellum directly. Neurons of the second order also enter the cerebellum from the vestibular nucleus, as well as from the spinal cord and from practically all of the somatic sensory centers of the brain; there is also a very important path from the cerebral cortex by way of the pons.

The cerebellum is attached to the brain stem by three stalks or peduncles on each side, the superior peduncle (brachium conjunctivum), the middle peduncle (brachium pontis), and the inferior peduncle (corpus restiforme). Figure 87, *A* illustrates diagrammatically the chief pathways which enter the cerebellum, and Fig. 87, *B* those by which nervous impulses leave it. We cannot here describe these connections in detail but can mention a few only of their general features.

The cerebellum, as already stated, receives afferent impulses from all of the important somatic sensory centers and also from the cerebral cortex. The afferent fibers from the spinal cord and brain stem enter by the superior and inferior peduncles. The pons is an eminence under the upper part of the medulla oblongata (Fig. 53) which contains gray centers (the pontile nuclei). Fibers pass into the pontile nuclei from the association centers of the cerebral cortex by way of the cortico-pontile tracts, and from the motor areas of the cerebral cortex by way of collateral branches from the cortico-spinal tract as it passes through the pons. These nervous impulses enter the cerebellar hemispheres from the pons by the middle cerebellar peduncles.

Fibers leave the cerebellum by all three peduncles for the motor centers of the brain stem (the cerebello-tegmental tracts, Fig. 87, *B*), and a much larger number leave by the superior peduncle for the red nucleus (nucleus ruber, Fig. 75) and adjacent parts of the brain stem, these fibers first crossing to the opposite side of the brain in the cerebral peduncle under the aqueduct of Sylvius. From the red nucleus fibers pass

downward into the spinal cord (rubro-spinal tract) and upward to the cerebral cortex.

Many of the tracts connecting with the cerebellum are uncrossed, thus differing from those of the cerebral cortex which are all made with the opposite side of the body. The symptoms of local injury of one cerebral hemisphere are, accordingly, usually manifested on the opposite side of the body from the lesion, while the symptoms of cerebellar disease are generally obscurely localized or are manifested on the same side as the lesion. But some of the cerebellar connections are crossed and others, like the dorsal spino-cerebellar and vestibulo-cerebellar tracts, which enter the cerebellum uncrossed may effect connection with the opposite side within the substance of the cerebellum. The following cerebellar tracts decussate outside the cerebellum:

The olivo-cerebellar tract arises from the inferior olive, crosses to the opposite side in the interolivary space, penetrates the other olive without effecting functional connection with it, and then enters the cerebellum through its inferior peduncle (Figs. 72 and 87, *A*). The cerebral cortex sends large descending cortico-pontile tracts to the pons of the same side (Figs. 75 and 87, *A*). Here there is a synapse in the pontile nuclei, whose neurons discharge into the opposite cerebellar hemisphere through the tractus ponto-cerebellaris in the middle cerebellar peduncle. The efferent path from the cerebellum to the red nucleus contained within the superior cerebellar peduncle decussates in the cerebral peduncle before entering the red nucleus. Important evidence regarding these decussations and the connections of the cerebellum with the brain stem in general is furnished by a case of defective development of the cerebellum on one side described by Strong (1915).

The connections just described illustrate some of the pathways by which the cerebellum is able to reinforce, coördinate, or otherwise modify the somatic motor mechanisms. There is an immense amount of potential nervous energy always available in the neurons of the cerebellar cortex, and the cerebellum appears to be constantly exerting a stimulating or tonic effect upon the body muscles. An injury to the cerebellum (especially an unsymmetric lesion) produces motor incoördination, and the total removal of the cerebellum results in loss of muscular tone and great weakness, though there is no abolition of any particular motor functions. The cerebellar cortex and the cerebral cortex are very intimately connected by large fiber tracts, and each apparently exerts an important physiological effect upon the other. But the exact nature of this reciprocal control is still obscure.

The cerebellar cortex differs from the cerebral cortex in the form and arrangement of its neurons and also, further, in that

it is structurally similar throughout its entire extent. The cerebral cortex, on the other hand, shows differences in the forms and arrangements of its neurons in different regions, and this is correlated with a regional localization of diverse functions (pp. 305, 316). There is some evidence that different parts of the cerebellar cortex exert a dominant regulatory influence over particular large groups of muscles; but this localization of function is of a very general sort and is by no means so precise as the localization of voluntary motor centers in the cerebral cortex. Moreover, the physiological influence of the cerebellum upon movement is of a very different sort from that of the cerebral cortex.

The mammalian cerebellum consists of a median lobe, the worm (vermis), and two larger cerebellar hemispheres. The vermis alone is well developed in lower vertebrates (from fishes to birds, see Fig. 43, p. 119). In different mammals the size of the pons and brachium pontis is proportional to that of the cerebellar hemispheres, and all of these vary in proportion to the size of the cerebral cortex. The pons and cerebellar hemispheres, therefore, are in a general way dependencies of the cerebral cortex (see p. 122), and probably are concerned chiefly with the coördination of voluntarily excited movements. These voluntary acts, however, do not differ on the motor side from similar movements which are reflexly excited; and in the actual functioning of the human cerebellum it is probable that its control of motor coördination is quite independent of the mode of excitation of the movements—whether reflex or voluntary. In other words, the anatomical distinction between vermis and cerebellar hemispheres has very limited physiological significance. This applies especially to the superior part of the cerebellum. The inferior part of the vermis, as we shall see, has more physiological individuality.

The comparative anatomy and comparative embryology of the cerebellum have recently been carefully studied by Elliot Smith, Bolk, and Rynberk. They have shown that its anatomical subdivisions, as named by the B. N. A. have no especial significance. The nomenclature of the B. N. A. and of Bolk and some other students are contrasted in Fig. 88.

By comparing the sizes and arrangement of the parts of the cerebellum, as Bolk enumerates them, in various animals with different modes of life this author concludes that there are coördination centers in the cerebellum for particular groups of muscles, whose arrangement in man is represented in Fig. 88.

Van Rynberk and André-Thomas and Durupt tested the truth of this conclusion experimentally by extirpating these areas in animals and observing the resulting symptoms, finding that Bolk's scheme in general is correct. Bárány and other clinical neurologists by observing the symptoms resulting from localized lesions of the human cerebellum have been led to similar conclusions.

As a result of these studies we conclude that the distinction between vermis and cerebellar hemispheres in general has little physiological significance. The most important landmark in the cerebellum is Bolk's sulcus primarius (the fissura prima of Elliot Smith) which separates a lobus anterior from a lobus posterior, the former being an unpaired center for the control of movements of the head. Behind the sulcus primarius on the dorsal surface is the lobulus simplex, a similar unpaired center for movements of the neck. Behind this is a median center for the control of bilateral movements of the limbs (the tuber vermis of the B. N. A., Fig. 88, *C*). Along the caudal and inferior faces of the cerebellum is a median center for movements of the trunk (pyramis, uvula and nodulus of the B. N. A.). This is largely concerned with movements of equilibration. In the cerebellar hemisphere of each side is a center for the control of unilateral movements of the limbs. The arm area is on the dorsal and caudal surface. The leg area in man has not been clearly determined, but by analogy with other mammals it probably lies as indicated in Fig. 88, *B*. The paramedian lobule (tonsilla of the B. N. A.) and the flocculus together form the formatio vermicularis and in lower mammals apparently are concerned with tail movements. Their significance in man is obscure.

This functional localization is in the cerebellar cortex. From what we know of the fiber connections of the cerebellar

cortex it may be inferred that the dentate nucleus is largely concerned with the coördination of movements of the arm and hand of the same side, while the roof nuclei in the inferior

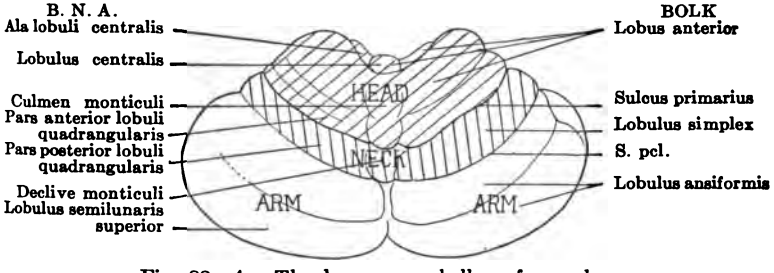

Fig. 88, *A*.—The human cerebellum from above.

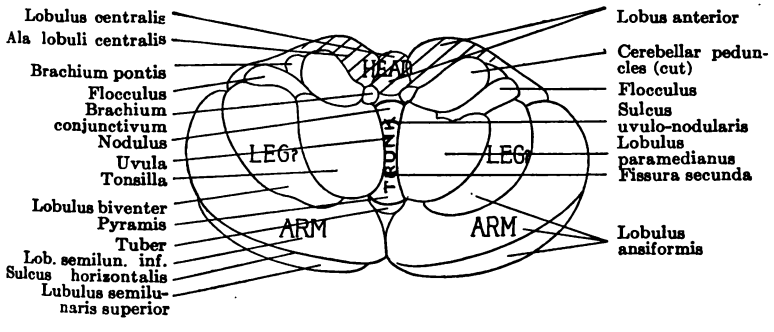

Fig. 88, *B*.—The human cerebellum from below.

In these two diagrams the principal subdivisions of the cerebellum are indicated and the B. N. A. names are designated at the left. At the right are the names given by Bolk to these structures and one fissure not named by Bolk, the sulcus postclivalis (*S.pcl.*), as named by Symington in Quain's Anatomy. The sulcus primarius of Bolk and Kuithan is the same as the furcal sulcus of Stroud, the fissura prima of Elliot Smith, and the sulcus preclivalis of Symington. The lobulus simplex of Bolk extends across the median plane and includes the declive of the B. N. A. in the vermis.

The functional localization within the cerebellar cortex as determined by Bolk, Rynberk, and others is also indicated on the figures. Head movements are controlled in the lobus anterior of Bolk, *i. e.*, all parts in front of the sulcus primarius. The lobus simplex controls neck movements. Arm and leg movements are controlled in the lobus ansiformis and trunk movements in the inferior vermis.

vermis are concerned with bilateral movements, especially those concerned with equilibration.

Ingvar has developed a different conception of cerebellar localization. He divides the cerebellum into anterior, middle, and posterior lobes. The first is the same as Bolk's. The posterior lobe includes the pyramis,

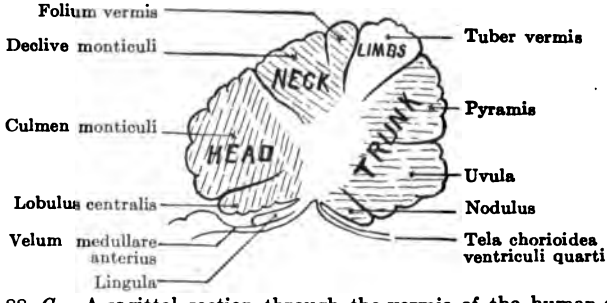

Fig. 88, *C*.—A sagittal section through the vermis of the human cerebellum. The B. N. A. names of the parts are given and also the functional localization as determined by Bolk, Rynberk, and others. The areas of the head and neck extend lateralward as indicated on Fig. 88, *A*. The area for control of movements of the trunk is limited to the inferior vermis. The area for the limbs in the tuber vermis is for the control of coördinated movements of both members of a pair, while the arm and leg areas shown in Figs. 88, *A* and 88, *B* control the separate movements of these limbs.

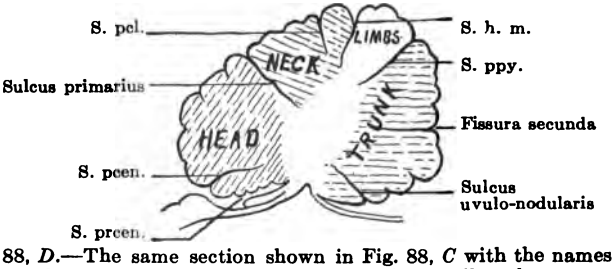

Fig. 88, *D*.—The same section shown in Fig. 88, *C* with the names of the cerebellar fissures. Bolk's names are printed in full; others are abbreviated. Between the lingula and the lobus centralis is the sulcus precentralis (*S.prcen.*) of Symington. Above the lobulus centralis is the sulcus postcentralis (*S.pcen.*) of Symington, or fissura preculminata of Elliot Smith. The sulcus primarius of Bolk is the fissura prima of Elliot Smith and the sulcus preclivalis of Symington. Above the declive is the sulcus postclivalis (*S.pcl.*) of Symington. Between the folium and the tuber is the sulcus horizontalis magnus (*S.h.m.*) of Symington. Between the tuber and the pyramis is the sulcus postpyramidalis (*S.ppy.*) of Symington. Below the pyramid is the fissura secunda of Bolk and Elliot Smith, or sulcus prepyramidalis of Symington. Between the uvula and the nodulus is the sulcus uvulo-nodularis of Bolk or sulcus postnodularis of Symington.

uvula, nodulus, flocculus, and paraflocculus. The middle lobe includes the lobulus simplex, tuber vermis, lobulus ansiformis, and tonsilla, thus embracing the greater part of the cerebellar hemispheres. The anterior

and posterior lobes form the primitive basal portion of the cerebellum which receives the afferent tracts from the spinal cord and brain stem and is probably concerned with the equilibratory adjustments of the body as a whole, motor coördination in the forward direction being regulated by the anterior lobe and in the backward direction by the posterior lobe. The middle lobe is of more recent evolutionary origin, receives the greater part of its nervous impulses from the cerebral hemispheres by way of the pons, and is concerned with the coördination of voluntary movements, chiefly of the limbs.

Recent clinical studies go to show that the fundamental function of the cerebellum is the coördination of separate movements into the complexes necessary for the performance of special acts, viz., *synergia*. This implies in simple acts the maintenance of proper balance between antagonistic muscles acting upon the same joint or member and in more complex acts the combination of many such "synergic units" simultaneously or successively as required to effect the appropriate motor adjustments. This synergic control seems to be effected in essentially the same way whether the movements are called forth reflexly or voluntarily.

The similarity of structure throughout the cerebellar cortex, in contrast with the diversity in the cerebral cortex, suggests that the *nature* of cerebellar function is essentially similar throughout and that the functional localization described is determined simply by differences in the lower motor centers with which the various cerebellar regions are connected.

The surface of the cerebellum is divided by deep fissures or sulci into narrow leaf-like subdivisions termed folia or gyri, so that when it is cut open across the median plane the cut surface looks somewhat like a sprig of the common evergreen cedar tree known as arbor vitæ. Hence this cut surface by the ancients was termed the arbor vitæ.

The gray matter of the cerebellum is partly superficial (this is the cortex to which reference has already been made) and partly in the form of deep nuclei embedded within the white matter. The largest of these deep gray centers are the dentate nuclei within the cerebellar hemispheres. Within the vermis are other smaller centers, called the roof nuclei, because they lie immediately above the fourth ventricle (nuclei emboliformis, globosus, and fastigii, see Fig. 96). Some of the afferent fibers

which enter the cerebellum end in these nuclei, but most of them end in the cortex. The efferent fibers, on the other hand, arise from the deep nuclei, especially the dentate nuclei (Fig. 87, *B*).

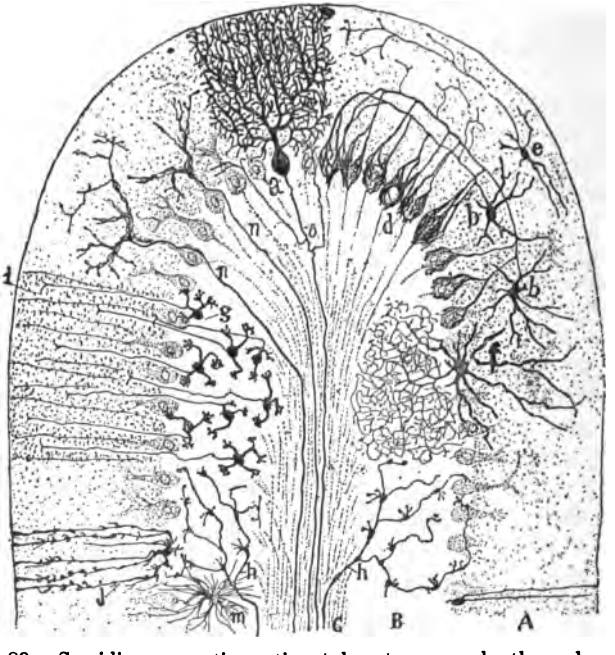

Fig. 89.—Semidiagrammatic section taken transversely through a folium of the cerebellar cortex (Golgi method): *A*, molecular layer, filled with axons of granule cells cut at right angles to their course; *B*, granular layer; *C*, white matter; *a*, Purkinje cell, with the dendrite, broadly spread out in the transverse plane (compare Fig. 15); *b*, basket cell (compare Fig. 16); *d*, terminal arborizations of the basket cells enveloping the bodies of the Purkinje cells; *e*, superficial stellate cells; *f*, Golgi cell of type II (see p. 45); *g*, granule cells with their axons ascending and bifurcating in the molecular layer at *i*; *h*, mossy fibers; *j*, neuroglia cell; *m*, neuroglia cell; *n*, climbing fibers. (After Ramón y Cajal.)

The cerebellar cortex has three distinct layers. External to the central white matter (Fig. 89, *C*) is a wide layer composed of very minute granule cells (Fig. 89, *B*) densely crowded together, with scanty cytoplasm, short, claw-like dendrites, and slender unmyelinated axons which ascend to the superficial

molecular layer (Fig. 89, *A*), where they bifurcate (their branches running lengthwise of the folium) and end among the dendrites of the Purkinje cells, to be described immediately. The middle layer of the cortex is composed of a single row of Purkinje cells (Fig. 89, *a*); these have large globose bodies with massive bushy dendrites directed outward and slender axons directed inward. These axons are myelinated and constitute the chief efferent pathway from the cortex; they do not, however, leave the cerebellum, but end in the deep gray nuclei (chiefly the dentate nuclei), from which other neurons carry the impulses out of the cerebellum. The dendrites of the Purkinje cells are widely expanded transversely to the length of the folium, but are very narrow in the opposite direction; thus each cell comes into contact with the largest possible number of axons of the granule cells which run lengthwise of the folium. The outermost or molecular layer contains the dendrites of the Purkinje cells, termini of the axons of the granule cells and of other fibers, and a small number of neurons with short axons, among which are the basket cells illustrated in Figs. 16 and 89, *b*.

Afferent fibers terminate in the cerebellar cortex in two ways. They may pass directly out to the molecular layer as ascending or climbing fibers, where they end in very intimate relation with the dendrites of the Purkinje cells (Figs. 15 and 89, *n*), or they may end as moss fibers (Fig. 89, *h*) among the cells of the granule layer. Here the granules take up the nervous impulses and deliver them to the dendrites of the Purkinje cells. Ramón y Cajal is of the opinion that the moss fibers are the terminals of the afferent fibers of the inferior cerebellar peduncle, and that the ascending fibers are the terminals of the fibers from the middle peduncle (brachium pontis).

Since each fiber from the inferior peduncle branches extensively and reaches many granule cells in widely separated parts of the cerebellum, and since the axon of each granule cell reaches the dendrites of a very large number of Purkinje cells, a single incoming nervous impulse may excite a very large number of Purkinje cells, and thus its physiological effect may be greatly enhanced. The same result is also secured by the

action of the basket cells (Fig. 89, *b*) and other forms of neurons with short axons within the cortex (Fig. 89, *e*, *f*), each of which may discharge powerful impulses directly upon several Purkinje cells. The axons of the Purkinje cells themselves also give off collateral fibers into the granular layer, whose neurons discharge back into the Purkinje cells again. In all of these ways provision is made for the diffusion, summation, and reinforcement of stimuli during the process of their transmission through the cerebellar cortex, and also for prolongation of motor reactions which would otherwise soon subside, and for the maintenance of muscular tone.

This type of reaction has been termed "avalanche conduction" (see p. 107), and its mechanism here is similar to that found in the olfactory bulb (p. 244), but much more complex. It is probable that the reciprocal relation between the cerebellum and the cerebral cortex is of a similar sort, all cortical activities exciting also the cerebellum and drawing therefrom additional nervous energy as needed to maintain the tone of the reacting mechanism; and voluntary movements excited by the cortico-spinal or pyramidal tract from the cerebral cortex (see p. 319) are under especially direct proprioceptive control from this source.

The relationships of the centers of the brain stem, the cerebral cortex, and the cerebellum may be illustrated somewhat crudely by the analogy of the three chief departments of the national government. The reflex centers of the brain stem correspond to the legislative branch of government, determining in advance by virtue of their innate structure what actions may appropriately be performed in each particular type of frequently recurring situation. The cerebral cortex is a sort of glorified judicial branch of government, interpreting the decrees of the legislative centers, integrating the behavior by combining its elements into coöperating systems in view of all the factors of present and past experience, and with extensive powers of veto over inappropriate reactions which may have been inaugurated by the lower centers. The cerebellum is the great administrative office which attends to the details of the proper execution of the acts which have been previously determined upon and initiated in the other departments of government.

Summary.—The vestibular apparatus and the cerebellum are genetically and physiologically very closely related. The semicircular canals are the most highly differentiated proprioceptive end-organs, serving chiefly the functions of equilibration and the maintenance of muscular tone. These reactions are, for the most part, unconsciously performed and there is no important cortical path from the vestibular nuclei. These nuclei effect reflex connections with the motor centers of the spinal cord and medulla oblongata, especially the eye-muscle nuclei, and with the cerebellum.

The cerebellum has been developed out of the primary vestibular area for the more perfect coördination and integration of the somatic motor reactions and for strengthening these reactions. It receives afferent fibers from all somatic sensory centers, and in mammals it is also very intimately connected with the cerebral cortex, these two higher centers appearing always to act conjointly. The cerebellum discharges into all of the somatic motor centers and assists in preserving the proper balance of muscular contraction and in the maintenance of muscular tone.

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CHAPTER XIII

THE AUDITORY APPARATUS

THE human organ of hearing consists of the external ear, bounded within by the drum membrane (tympanic membrane, membrana tympani); the middle ear, a cavity filled with air which communicates with the pharynx through the auditory

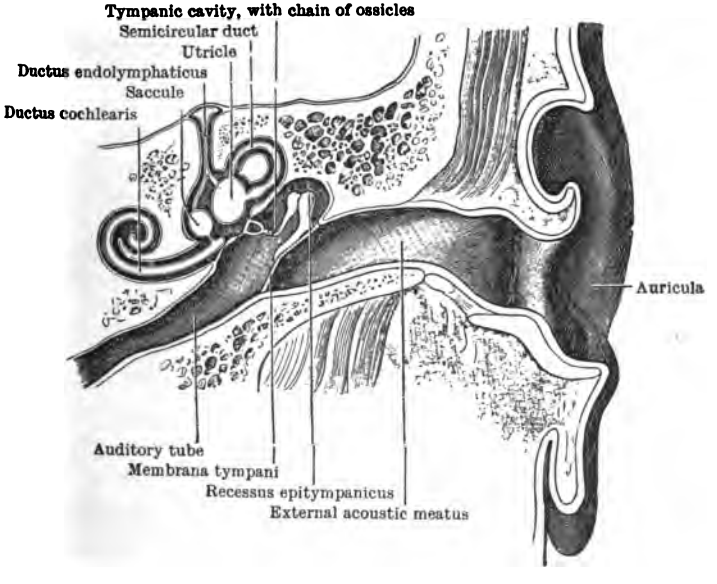

Fig. 90.—Diagrammatic view of the parts of the human ear. (From Cunningham's Anatomy.)

or Eustachian tube and contains the auditory ossicles; and the internal ear, a complex bony chamber, the bony labyrinth, within which is the membranous labyrinth containing the specific receptors or sensory surfaces of the internal ear

(Fig. 90). The tympanic membrane receives the air waves which form the physical stimuli of sound (pp. 75 and 92). These vibrations are then transmitted (and at the same time intensified about thirty-fold) by the auditory ossicles of the middle ear to the liquid within the bony labyrinth.

The membranous labyrinth is of approximately the same shape as the bony labyrinth, but smaller, so that there is a space between the membranous labyrinth and the enclosing bony wall. This space is filled with liquid, the perilymph, and the membranous labyrinth is also filled with liquid, the endolymph. In Fig. 90 the perilymphatic space is printed in black and the endolymphatic space in white. The parts of the membranous labyrinth are shown diagrammatically in Fig. 91.

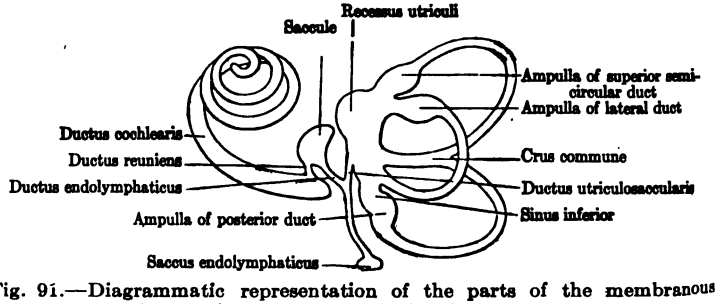

Fig. 91.—Diagrammatic representation of the parts of the membranous labyrinth. (From Cunningham's Anatomy.)

The membranous labyrinth is a closed sac which has four chief parts: (1) the utricle (recessus utriculi), with a patch of sensory epithelium, the macula utriculi; (2) the three semicircular canals (ductus semicirculares), each of which communicates at both ends with the utricle and has at one end a dilation (ampulla) containing a patch of sensory epithelium, the crista; (3) the saccule (sacculus) connected by a narrow ductus utriculosaccularis with the utricle and containing a patch of sensory epithelium, the macula sacculi; (4) the ductus cochlearis, which communicates by a narrow ductus reuniens with the saccule and is spirally wound to fit the bony cochlea, which is shaped like a snail shell. The ductus cochlearis (old name, scala media) is triangular in cross-

section (Fig. 92) and contains the specific auditory receptive epithelium in the spiral organ, or organ of Corti.

The organ of Corti is a very highly differentiated sensory epithelium which rests upon a firm basilar membrane (Fig. 92, membrana basilaris). Many details of the structure of this organ and the whole question of the mode of its functioning are still controverted. Figure 93 has been drawn for this work by Dr. O. Van der Stricht to illustrate his observations.

The sensory epithelium consists of non-sensory supporting cells of several sorts and four or five rows of specific sensory cells, the auditory hair cells. The supporting cells assume various forms in different parts of the epithelium, and two rows of these cells are specially modified to form the firm inner and outer pillars, or rods, of Corti which incline toward each other to enclose the tunnel of Corti. The sensory cells are arranged

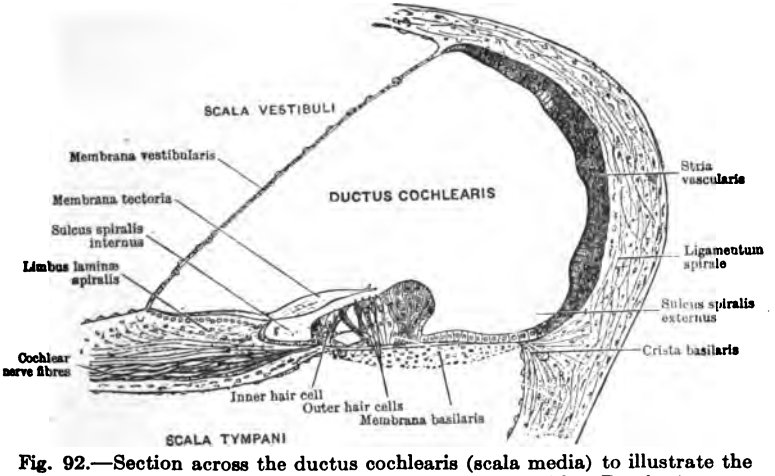

Fig. 92.—Section across the ductus cochlearis (scala media) to illustrate the relations of the spiral organ (organ of Corti). (After Retzius.)

in one row of inner hair cells and three or four rows of outer hair cells on opposite sides of the tunnel of Corti. These hair cells extend only part way through the thickness of the epithelium and the supporting cells below and between the outer hair cells are known as the cells of Deiters. Within each of these cells is a stiff axial filament which expands to form a chalice-like support under the base of a hair cell.

The fibers of the cochlear nerve pass outward from the axis of the spiral of the cochlea, then upward to traverse the tunnel of Corti. Here some turn to form a longitudinal trunk within the tunnel (Fig. 93, *N*). Fibers leave this trunk to cross the tunnel transversely and end in relation with the outer hair cells. The termini of the fibers of the cochlear nerve arborize around the bases of the hair cells in the same way that fibers of the vestibular nerve are related to the hair cells of the cristæ of the semicircular canals (Fig. 32, p. 94).

The tectorial membrane (membrana tectoria) is a delicate gelatinous mass resting upon the organ of Corti and intimately connected with the hairs of the hair cells. Its shape and properties have been carefully studied by Hardesty.

The development of the tectorial membrane has been restudied by Prentiss and Hardesty and still more recently by Van der Stricht. It first appears as a thin cuticular plate developed over the free ends of the columnar cells which form the inner or axial part of the epithelium on the basilar membrane. In the adult ear it retains its attachment to the limbus of the spiral lamina along the axial border of this epithelium, but becomes free from the cells which form the lining of the spiral sulcus. Prentiss describes the membrane as growing in thickness by the secretion of a cuticulum formed between the ends of the epithelial cells, thus giving to the mature membrane a chambered or honey-comb structure.

Van der Stricht confirms Prentiss' observation that the tectorial membrane arises from the epithelium lining the limbus of the spiral lamina, the future spiral sulcus and the organ of Corti, and he adds further details of the development and adult structure of this region. In early embryos the intercellular substance becomes condensed between the apices of the epithelial cells and forms the "terminal bars" which close the intercellular spaces. These bars take a large part in the development of the tectorial membrane and the fenestrated membrana reticularis of the organ of Corti. The tectorial membrane is made up of cylinders or prisms, the denser part of which (the walls) arises from the terminal bars and the more fluid part (their content) arises from the cytoplasmic apices of the subjacent epithelial cells. The membrana reticularis is represented by the primitive terminal bars, which at the level of the organ of Corti and after the development of the tectorial membrane become very thick, mainly around the apices of the hair cells, and give rise to the fenestrated membrane with two kinds of openings: rounded apertures through which project the hairs of the auditory hair cells and others of various shape and size which are closed by the apices of the supporting cells.

Regarding the functions of these parts, our present knowledge of the histological organization of the basilar membrane shows that it is structurally incapable of serving the function of tone analysis in the way postulated by Helmholtz' theory. The tectorial membrane is probably the medium through which sound waves are transmitted to the auditory receptors, viz., the hair cells. Shambaugh and Prentiss are of the opinion that the hairs of the hair cells are firmly attached to the tectorial membrane (Fig. 94), which has a semi-gelatinous texture and is capable of taking up sympathetically the vibrations of the endolymph within which it floats. According to this theory the tectorial membrane functions as a physical resonator, effecting tone analysis by responding in its various parts to tones of different pitch, depending on the size of the membrane. Tones of higher pitch would be taken up by the hair cells located near the beginning of the basal coil, those of lower pitch by the cells near the apex of the cochlea, where the tectorial membrane attains its maximum size.

Hardesty has constructed a large mechanical model to illustrate the probable working of the spiral organ and especially of the tectorial membrane. His artificial tectorial membrane can be excited to vibration by sound waves of different pitch and is capable of effecting a limited degree of tone analysis. Although the model gave some results which suggest the possibility that the tectorial membrane may act as a physical resona-

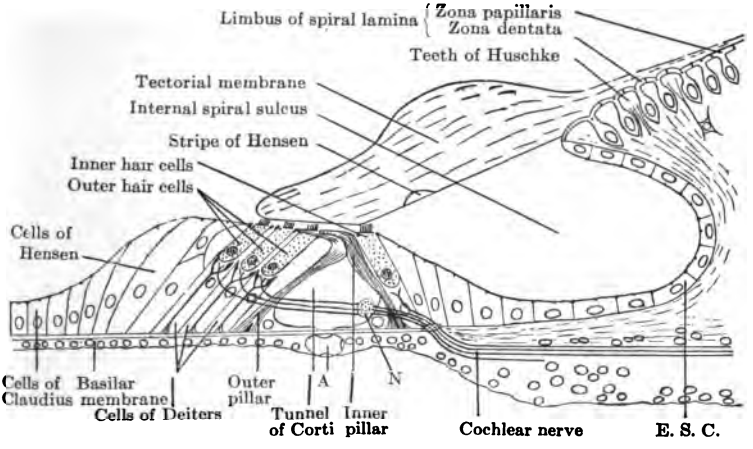

Fig. 93.—Diagrammatic cross-section of the spiral organ (organ of Corti) of the adult rat. The teeth of Huschke are represented as if cut transversely in a slightly different plane from the remainder of the section. The innervation is very diagrammatically indicated after the researches of Held (1902). Drawn by Dr. O. Van der Stricht (for further details see his paper (1918) cited in the appended bibliography). *A*, Spiral vessel; *E.S.C.*, epithelium of spiral sulcus; *N*, longitudinal nerve of tunnel of Corti.

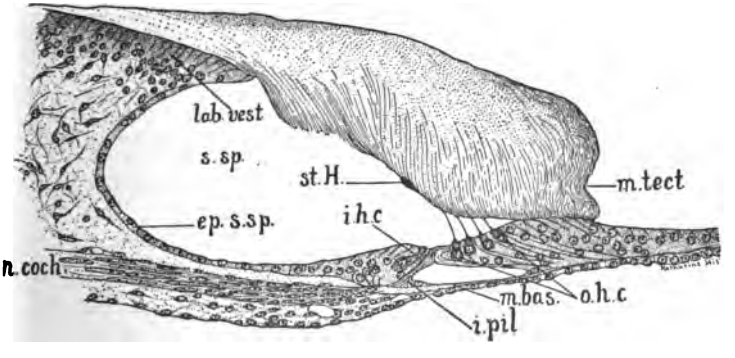

Fig. 94.—Section through the apical turn of the cochlea of the pig at about full term, showing outer auditory hairs embedded in the membrana tectoria: *ep.s.sp.*, epithelium of spiral sulcus; *i.h.c.*, inner hair cells; *i.pil.*, inner pillar; *m.bas.*, basilar membrane; *m.tect.*, membrana tectoria; *lab. vest.*, labium vestibulare; *n. coch.*, cochlear nerve; *o.h.c.*, outer hair cell; *s.sp.*, sulcus spiralis; *st.H.*, stripe of Hensen. (After C. W. Prentiss.)

tor in effecting tone analysis as suggested by Shambaugh, the entire artificial tectorial membrane is thrown into vibration by sounds of low pitch, and Hardesty is of the opinion that there is no apparatus in the internal ear capable of acting as a physical resonator. The problem of the mode function of the spiral organ is as yet unsolved.

In fishes the organs of the internal ear are intimately associated with an extensive series of subcutaneous canals containing numerous sense organs and with naked cutaneous sense organs of the same type, the entire complex forming the system of lateral line sense organs (see p. 120 and Fig. 95). The nerves which in fishes supply the lateral line sense organs (lateralis roots of the VII and X cranial nerves) and the organs of the internal ear (VIII nerve) are intimately associated and terminate together in the acoustico-lateral area of the medulla oblongata (Figs. 43 and 44, pp. 119, 120), and all of these end-organs have the same type of structure as those of the human internal ear (Fig. 32, p. 94).

The internal ears of fishes are essentially similar to those of man save that they lack the cochlea and the organ of Corti. They possess a small sense organ in the saccule, the lagena, supplied by a special branch of the VIII nerve (Fig. 95, *RL*), from which the cochlea of higher vertebrates has been developed. The researches of Parker have shown that fishes hear, though there is no evidence that they possess the power of tone analysis, and the sense organs of the saccule are the essential receptors for sound waves. The sense organs of the lateral line system are said by Parker to be sensitive to water vibrations of slower frequency than the sound waves to which the ear responds, while Hofer is of the opinion that these organs are stimulated only by streaming movements of the water in which the animals live. Probably the lateral line organs also participate in the equilibratory reactions of the fish.

Though our knowledge of the functions of the various parts of the acoustico-lateral system of fishes is still very imperfect, it is evident that all of these organs are both structurally and physiologically of common type, and it is probable that they have had a common evolutionary origin from a more generalized form of cutaneous tactile organ. This is the explanation of the intimate association in the human ear of sense organs of so diverse functions as the cochlea for hearing and the semicircular canals for equilibration, the former being an exteroceptor whose reactions may be vividly conscious, and the latter being a proprioceptor whose reactions are almost entirely unconsciously performed. For further consideration of the semicircular canals and their central connections see p. 202).

In the human body the cochlear and vestibular nerves are very intimately associated, but the embryological studies of Streeter and others have made it plain that these two nerves are really more distinct than was formerly supposed. The peripheral receptors of the cochlea and semicircular canals are obviously as dissimilar as are their functions, but the functional significance of the sensory organs of the utricle and saccule is more uncertain. The fact that fishes undoubtedly hear, notwithstanding their lack of cochlea or any other receptors more

complex than the sensory spots in the saccule, demonstrates the relatively late phylogenetic origin of the cochlear system

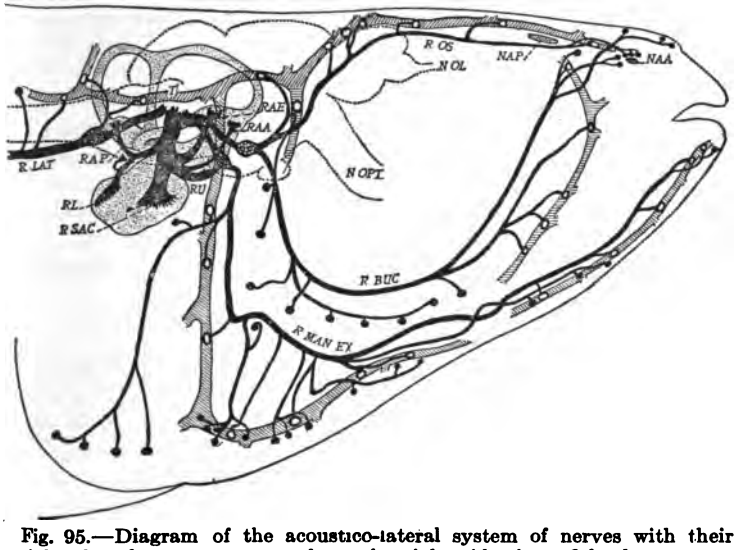

Fig. 95.—Diagram of the acoustico-lateral system of nerves with their peripheral end-organs, as seen from the right side, in a fish, the common silver-sides, Menidia (× 9). The relations here figured were reconstructed from serial sections by projection upon the sagittal plane. For the relations between the acoustico-lateral nerves and the other systems of nerves in this fish, see the more detailed chart from which this was drawn off, in the Journal of Comparative Neurology, vol. ix, 1899, plate 15; cf. also Fig. 65, p. 163, of this book. The dotted outline represents the position of the brain, the lateral line canals are shaded with cross-hatching, the internal ear is stippled, and the nerves are drawn in black. The organs of the lateral line system are drawn as black disks when naked on the surface of the skin, and as black circles when lying in the canals. *NAA*, anterior nasal aperture; *NAP*, posterior nasal aperture; *N OL*, olfactory nerve; *N OPT*, optic nerve; *RAA*, nerve of superior ampulla; *RAE*, nerve of lateral ampulla; *RAP*, nerve of inferior ampulla; *R BUC*, ramus buccalis of facial nerve; *RL*, nerve of the lagena (rudimentary spiral organ); *R LAT*, ramus lateralis of the vagus; *R OS*, ramus ophthalmicus superficialis of the facial nerve; *R MAN EX*, ramus mandibularis externus of the facial nerve; *R SAC*, nerve of the sacculus; *RU*, nerve of the utriculus; *T*, acoustico-lateral area. (After Herrick, from Wood's Reference Handbook of the Medical Sciences, Article, "Ear.")

from the vestibular, and has suggested to some physiologists that even in man these two systems are not wholly distinct, and that the sense organs in the saccule may also function as

a sound receptor. It is clear, however, that tone analysis is effected only in the cochlea.

The central connections of the cochlear and vestibular nerves are fundamentally different. The vestibular nerve terminates

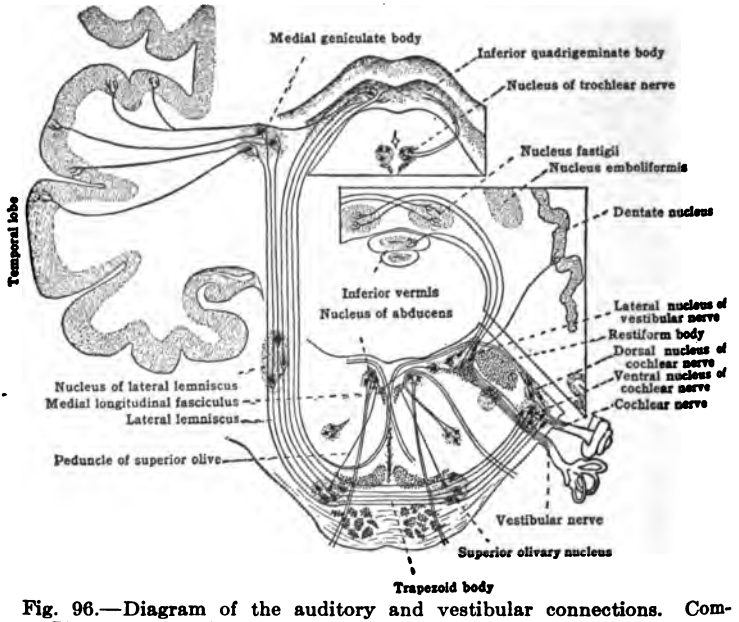

Fig. 96.—Diagram of the auditory and vestibular connections. Compare Figs. 71, 77, and 86. The fibers of the cochlear nerve enter the ventral and dorsal cochlear nuclei (the latter being termed the tuberculum acusticum) at the lateral border of the medulla oblongata. The auditory path now divides, one tract, the trapezoid body, passing ventrally through the pons to enter the lateral lemniscus of the opposite side, and the other passing dorsally through the acoustic medullary striæ (striæ medullares acustici) across the floor of the fourth ventricle and also entering the lateral lemniscus. These fibers may be interrupted by synapses in the superior olives, the nucleus of the lateral lemniscus or the inferior colliculus (inferior quadrigeminate body) before they reach the medial geniculate body of the thalamus, or they may pass by these nuclei without connecting with them. The fibers shown in the diagram as passing from the inferior quadrigeminate body to the temporal lobe of the cerebral cortex are probably interrupted by a synapse in the medial geniculate body. (From Morris' Anatomy.)

in reflex centers of the medulla oblongata and cerebellum (p. 204) with no important cortical connections, while the cochlear

nerve has, in addition to the important reflex connections in the oblongata and midbrain, the much stronger ascending pathway of the lateral lemniscus directly to the medial geniculate body of the thalamus, and thence to the temporal lobe of the cerebral cortex (see p. 171 and Figs. 75, 77, 80, 96). Some of the fibers of the lateral lemniscus are interrupted in the inferior colliculus, which is an important auditory reflex center.

Reflex responses to auditory stimuli may be effected by collateral connections made at various points along the course of the main cortical path in the lateral lemniscus. Some of these points of synapse are, the superior olives, nuclei of the trapezoid body, nuclei of the lateral lemniscus, and inferior colliculus (Fig. 96). Most of these collateral connections are relatively short tracts connecting directly with the adjacent motor nuclei of the midbrain and medulla oblongata. Spinal reflexes are made by the tecto-spinal tract from the inferior colliculus, part of these fibers first decussating in the dorsal tegmental decussation of the midbrain (Figs. 59, 73, 75).

Summary.—The human ear has three parts: (1) the external ear, for receiving sound waves from the air; (2) the middle ear, for intensifying the vibrations and transmitting them to (3) the internal ear, which is filled with liquid and contains sense organs of uncertain function in the utricle and saccule, sense organs for equilibration in the semicircular canals, and the spiral organ (organ of Corti) in the cochlea for tone analysis. The spiral organ is a complicated epithelial structure resting on a basilar membrane and consisting of supporting cells of diverse kinds, the hair cells (which are the specific receptors and receive the endings of the fibers of the cochlear nerve), and the tectorial membrane. Shambaugh is of the opinion that the tectorial membrane is capable of responding in its various parts to different vibration frequencies, and that the hair cells are stimulated through their hairs which are attached to the tectorial membrane.

In fishes the organ of hearing is much simpler than in man, the semicircular canals are, however, similar, and there is, in addition, an elaborate system of lateral line sense organs whose functions seem to be intermediate between the tactile and auditory organs. It is probable that these three systems of sense

organs were derived phylogenetically from some more generalized form of cutaneous tactile organ. This accounts for the intimate association in the human ear of organs of so diverse functions as the semicircular canals and the cochlea.

The central connections of the vestibular and cochlear nerves are very different, the former effecting chiefly reflex connections for equilibration in the medulla oblongata and cerebellum, and the latter both reflex connections in the brain stem and cortical connections through the lateral lemniscus, medial geniculate body of the thalamus and auditory radiations, for conscious sensations of hearing.

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CHAPTER XIV

THE VISUAL APPARATUS

THE eye is the most highly specialized sense organ in the human body, and in other respects it occupies a very unique position. The essential receptive part of the eye is in the retina. But the retina is much more than this; it is really a part of the brain, and the so-called optic nerve is a true cerebral tract. This is evident from a consideration of the embryologic development of the retina.

In the early embryonic stages the neural tube expands laterally in the position of the future thalamus, and from the upper part of this region a "primary optic vesicle" is evaginated from the lateral wall on each side

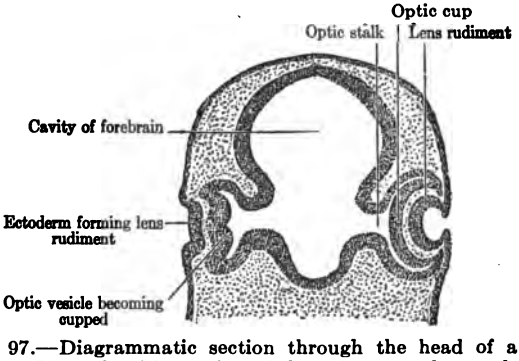

Fig. 97.—Diagrammatic section through the head of a fetal rabbit to illustrate the mode of formation of the primary and secondary optic vesicles and of the lens of the eye. The right side of the figure is drawn from a more advanced stage than the left side. (From Cunningham's Anatomy.)

(Figs. 46, 47, 49, 97). The optic vesicle grows outward toward the skin and assumes the form of a hollow sphere, whose cavity remains in communication with that of the third ventricle by a hollow stalk (Fig. 97). While the formation of the primary optic vesicle is in progress the overlying ectoderm (outer skin) is thickened and finally invaginated to form the lens of the eye, the optic vesicle collapses so that its cavity is obliterated by the apposition of its lateral and medial walls, and a secondary cavity (the secondary optic vesicle or optic cup) is formed whose walls are two-layered, being composed of both the original lateral and medial parts

of the primary optic vesicle (Fig. 97, on the right side). This secondary cavity contains the vitreous humor in the adult eye; the layer of the secondary optic vesicle which borders the vitreous humor forms the retina; the outer layer of the vesicle forms the pigment layer of the retina; and the stalk forms the optic nerve by the ingrowth of fibers throughout its length from the retina and brain (Fig. 100).

The retina, then, is as truly a part of the brain as is the cerebral hemisphere and its structure is, in general, similar to that of other parts of the brain. There are supporting cells, the fibers of Müller (Fig. 98, *M*), and neuroglia elements (Fig. 98, *d.s.* and *s.s.*), and lying among these are the neurons. The latter can be classified in general in four groups: (1) the rods and cones (Fig. 98, *A*); (2) the bipolar cells (Fig. 98, *D*); (3) the so-called ganglion cells which give rise to fibers of the optic nerve (Fig. 98, *F*); (4) horizontally disposed correlation neurons (Fig. 98, *h*). All of these types except the third are intrinsic to the retina, *i. e.*, they send none of their fibrous processes beyond the limits of the retina itself. The axons of the neurons of the third type pass out of the retina and form the so-called optic nerve, terminating in the thalamus or midbrain.

Immediately external to the nervous layer of the retina is the pigment layer (Figs. 99, 100), which is formed from the outer epithelial layer of the secondary optic vesicle (Fig. 97). Figure 99 illustrates the ten layers of the retina as figured by the older histologists, and Fig. 98 illustrates the relations of some of the nervous elements as revealed by the Golgi method. It is evident that the "nuclear" or "granular" layers are characterized chiefly by the presence of the cell bodies of the neurons and their nuclei, while the "molecular" layers are composed chiefly of the fibrillar nerve-endings which form the synapses between the various groups of neurons.

The rods and cones of the retina are the receptors and also the neurons of the first order in the optic path. Their free ends project through the external limiting membrane into the pigment layers. Rays of light which pass through the dioptric apparatus (lens, humors, etc.) of the eyeball must penetrate also the entire thickness of the retina (which is very transparent) before they reach these receptors (Fig. 100).

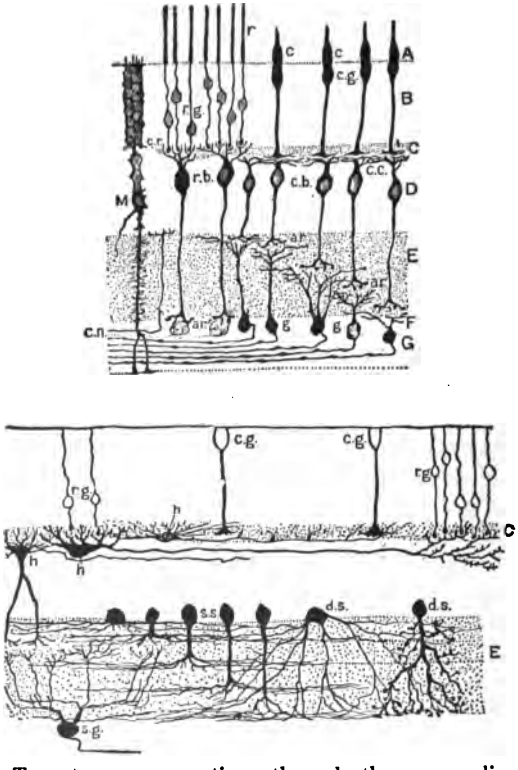

Fig. 98.—Two transverse sections through the mammalian retina: *A*, Layer of rods and cones; *ar*, internal arborizations of bipolar neurons related to the cones; *ar'*, internal arborizations of bipolar neurons related to the rods; *B*, outer nuclear layer; *C*, outer molecular layer; *c*, cones; *c.c.*, contact of bipolar neurons with branches of the cone fibers; *c.b.*, bipolar neurons related to cones; *c.g.*, cone granules or nuclei of cones; *c.n.*, centrifugal nerve-fiber; *c.r.*, contact of bipolar neurons with ends of rod fibers; *D*, inner nuclear layer; *d.s.*, diffuse neuroglia elements; *E*, inner molecular layer; *F*, ganglionic layer; *G*, layer of nerve-fibers; *g*, neurons of the ganglionic layer; *h*, horizontal cells; *M*, supporting fiber of Müller; *r*, rods; *r.b.*, bipolar neurons related to rods; *r.g.*, rod granules or nuclei of rods; *s.g.*, stratified ganglion cells; *s.s.*, stratified neuroglia elements. (After Ramón y Cajal.)

The peripheral ends of the rods contain a pigment, the visual purple or rhodopsin, which is chemically changed by light rays and is supposed to function as the exciting agent for nervous impulses of sensibility to light in the rod cells. But some recent experiments suggest that the visual purple is concerned with the adaptation of the eye to different intensities

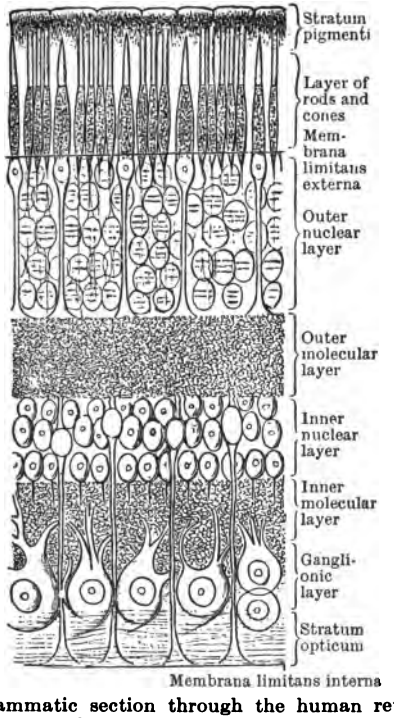

Fig. 99.—Diagrammatic section through the human retina to illustrate the ten layers as commonly enumerated. (After Schultze, from Cunningham's Anatomy.)

of light rather than with the specific receptor function itself, and the question is still undecided. The brown pigment of the pigment layer is probably also concerned with light adaptation.

The exact mechanism through the agency of which the rods and cones are excited to nervous activity by light is still obscure; but when the rods and cones are once activated, they

may transmit their nervous impulses across synapses in the external molecular layer to neurons of the second order whose cell bodies lie in the internal granular layer. The neurons of the internal granular layer are of diverse sorts, some of them spreading the nervous impulse laterally (probably for summation effects in weak illumination), but most of them conducting radially and effecting synaptic connection with the dendrites of the "ganglion cells of the retina." The latter are neurons of the third order whose axons form the larger

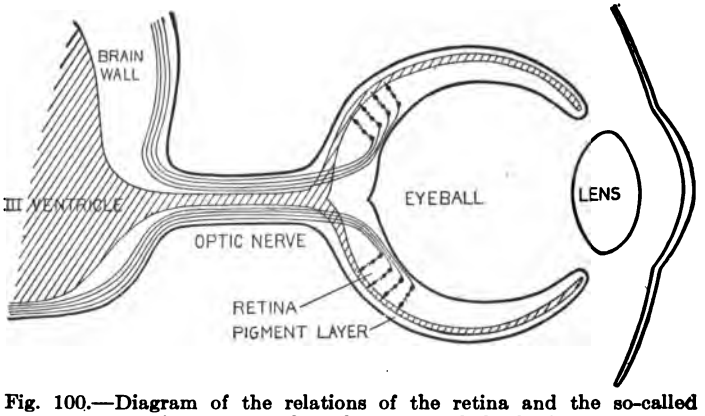

Fig. 100.—Diagram of the relations of the retina and the so-called optic nerve to the other parts of the brain.

part of the fibers of the so-called optic nerve, which is really not a peripheral nerve at all, but a true cerebral tract.

The fibers of the "optic nerve," having reached the ventral surface of the brain, enter the optic chiasma, where part of them cross to the opposite side of the brain, while others enter the "optic tract" of the same side. From the chiasma a big tract of crossed and uncrossed optic fibers passes upward and backward across the surface of the thalamus, where they divide into two groups. Some terminate in the pulvinar and lateral geniculate body which form the postero-dorsal part of the thalamus (Figs. 53, 76, 77); others pass these structures to end in the roof of the superior colliculus of the midbrain, *i. e.*, in the optic tectum. The latter connection

is for responses of purely reflex type, chiefly those concerned with the movements of the eyeballs and accommodation of the eyes; the thalamic connection is a station in the cortical visual path.

From these relations it follows that there is nothing in the visual organs which corresponds to a peripheral nerve. The retina as a part of the brain is directly excited by the light waves which penetrate its substance. The so-called optic nerve is a tract within the brain, whose fibers for the most part come from visual neurons of the third order in the retina, though there are others also which come from the brain and pass outward to end by free arborizations within the retina (Fig. 98, *c.n.*). The function of these centrifugal fibers to the retina is unknown. Identically the same nerve-fibers which make up the so-called optic nerves peripherally of the optic chiasma are called the optic tracts centrally of that point. It would be more logical to name these fibers optic tracts for their entire length, these tracts being very similar to those of the lemniscus systems. Like the lemniscus fibers, they decussate completely in the optic chiasma in lower vertebrates before terminating in the thalamus and midbrain. It is only in animals with an overlapping of the fields of vision of the two eyes and stereoscopic vision that the decussation of the optic tracts in the chiasma is incomplete.

The significance of the crossed and uncrossed fibers of the optic tracts is seen in Fig. 101. In this diagram the shaded portions of the retinæ receive their light from the left side of the median plane of the body; the unshaded portions, from the right side. The nasal part of each retina receives visual images from objects lying in the same side of the body exclusively, *i. e.*, from the temporal portion of the visual field, while the temporal part of the retina may receive images from objects on the opposite side of the body. Accordingly, in order that the visual images derived from all objects lying on one side of the body may be represented by nervous excitations within the opposite half of the brain, it is necessary that the nerve-fibers from the nasal part of each retina cross in the chiasma, while those from the temporal part pass through the chiasma without decussation.

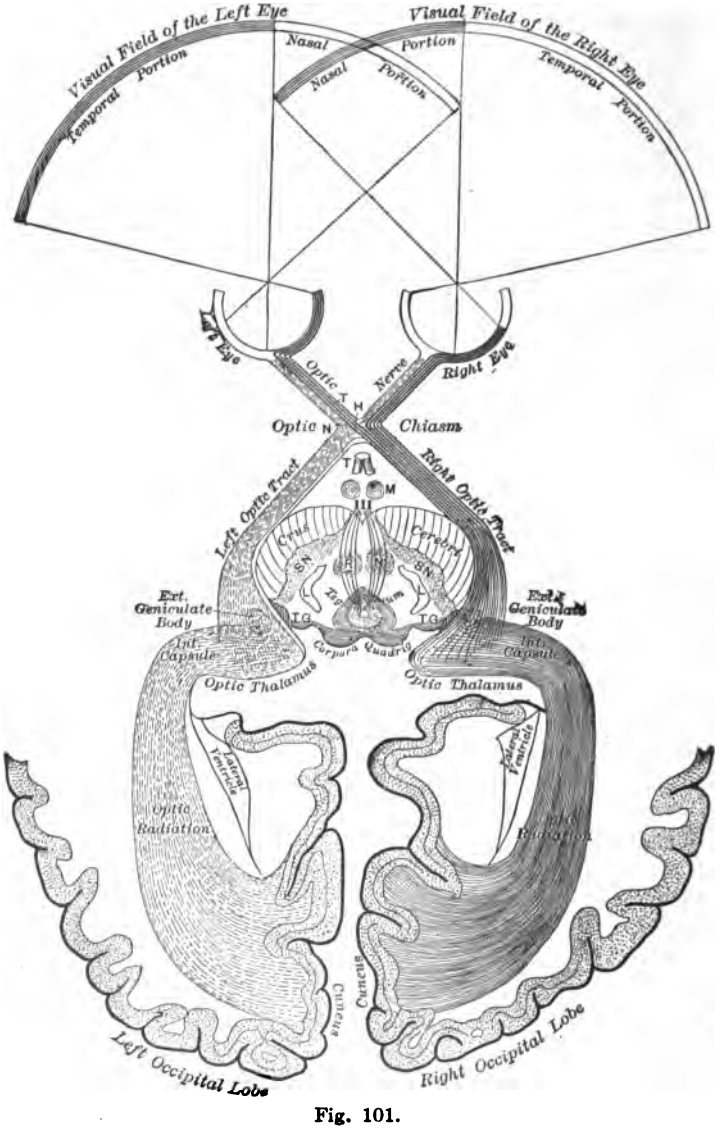
Visual Field of the Left Eye
Visual Field of the Right Eye
Temporal Portion
Nasal Portion
Nasal Portion
Temporal Portion
Left Eye
Right Eye
Optic Nerve
Optic Chiasm
Left Optic Tract
Right Optic Tract
Crus Cerebri
Ext. Geniculate Body
Ext. Geniculate Body
Int. Capsule
Int. Capsule
Corpora Quadrig
Optic Thalamus
Optic Thalamus
Lateral Ventricle
Lateral Ventricle
Optic Radiation
Cuneus
Cuneus
Left Occipital Lobe
Right Occipital Lobe

Fig. 101.

The reflex optic centers in the roof of the midbrain occupy most of the colliculus superior, which corresponds to the optic lobe of the fish brain (Figs. 43, 44). Here visual impressions are brought into physiological relations with those of the tactual and auditory systems received by the lemnisci. The chief efferent pathway from this center is by way of the underlying cerebral peduncle (Fig. 75). Here reflex connections are effected directly with the nuclei of the III and IV cranial nerves for the eye muscles, and through the fasciculus longitudinalis medialis with the centers for all other cranial and spinal muscles. This fasciculus is a strong bundle composed of both descending and ascending fibers whose function is the general coördination of reflex motor responses, and in particular those of the conjugate movements of the two eyes (see p. 204). Reflex movements of the muscles of the trunk and limbs in response to visual stimuli are effected chiefly through the tecto-spinal tract, this tract conveying fibers also for auditory reflexes from the inferior colliculus (p. 227).

The accommodation of the eye for distance is effected by changes in the curvature of the lens, and the adaptation for differences in illumination is effected in part by changes in the diameter of the pupil (this is in addition to the changes in the retinal pigment referred to on p. 233 and to changes in the rods and cones and other neurons of the retina which may be excited by the centrifugal fibers from the brain to the retina referred to on p. 235). The nerves controlling the movements of the lens and the pupillary reactions belong to the visceral motor system. They leave the central nervous system in part through the oculomotor nerve and in part (for dilation of the pupil) from the lower cervical region of the spinal cord. The latter fibers pass by way of roots of spinal nerves into the superior cervical sympathetic ganglion (p. 263 and Fig. 41, p. 115) and then forward to the eyeball. We cannot here enter into

Fig. 101.—A diagram of the visual tract, illustrating the significance of the partial decussation of nerve-fibers in the optic chiasma so as to ensure the representation in the cerebral cortex of nervous impulses excited by objects on the opposite half of the body only. *III*, Oculomotor nerve; *L*, medial lemniscus; *M*, mammillary bodies; *RN*, red nucleus (nucleus ruber); *SN*, black substance (substantia nigra); *TG*, optic tract to corpora quadrigemina (cf. Fig. 75). (From Starr's Nervous Diseases.)

further details of the mechanism of accommodation or of the dioptric apparatus and the accessory parts of the eye; see the larger text-books of anatomy and physiology.

The thalamic connections of the optic tracts in the lowest vertebrates are very insignificant, collaterals of these fibers being given off to terminate in the unspecialized correlation centers of the dorsal part of the thalamus. But in all forms with a differentiated cerebral cortex these thalamic optic connections assume greater importance, a special region in the dorsal part of the thalamus being set apart for their use. Thus arose the lateral geniculate body, and in higher mammals this

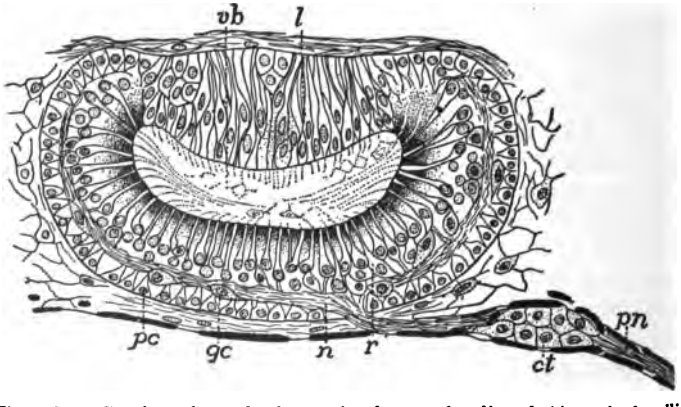

Fig. 102.—Section through the parietal eye of a lizard (Anguis fragilis): *ct*, connective-tissue cells around nerve; *gc*, ganglion cells; *l*, lens; *n*, nerve-fibers; *pc*, pigment cells; *pn*, parietal nerve from the parietal eye to the brain; *r*, retinal cells; *vb*, vitreous body. (After Nowikoff.)

is supplemented by the pulvinar. These centers are, in the strict sense of the word, cortical dependencies, for they attain to only very insignificant proportions in forms with rudimentary cerebral cortex, but increase in proportion to the elaborating of the visual cortex (see p. 122).

The early steps in the evolution of the eyes of vertebrates are imperfectly understood. In structure and mode of function the vertebrate eyes are unlike those of any of the invertebrate animals. The experiments of Parker and others have shown that the skin of many aquatic vertebrates among the fishes and amphibians is sensitive to light, and it has been supposed that the vertebrate retina was differentiated from such

cutaneous photoreceptors. But it seems more probable (Parker, 1908) that the vertebrate organs of vision were developed from the first within the central nervous system.

Some of the fishes and reptiles possess, in addition to lateral eyes of typical form, a median eye, the parietal or pineal eye (Fig. 102), which is developed from a tubular outgrowth from the roof of the diencephalon (the pineal organ or epiphysis, p. 177); this extends dorsalward from the brain through a special foramen in the skull to reach the skin in the center of the top of the head. The functions and evolutionary significance of this eye are shrouded in mystery.

Summary.—The retina is developed as a lateral outgrowth from the early neural tube and throughout life retains its character as a part of the brain, the "optic nerve" being really a correlation tract comparable with the lemniscus systems. The rods and cones of the retina are the photoreceptors and also the neurons of the first order in the optic path. The "optic nerve" contains neurons of the third order from the retina to the thalamus and midbrain, and also centrifugal fibers from the midbrain to the retina. In lower vertebrates the fibers of the optic path decussate completely in the optic chiasma, but in those mammals whose fields of vision overlap there is an incomplete decussation so as to ensure the representation of the field of vision of one side completely in the opposite cerebral hemisphere. Those fibers of the optic tract which terminate in the midbrain effect various kinds of reflex connections, while those which terminate in the thalamus effect cortical connections. The parietal or pineal eye of some fishes and reptiles is apparently functional as an organ of vision which was developed quite independently of the lateral eyes.

Literature

In this chapter we have not attempted to present a systematic description of the structure of the eye or of the functions of the retina and theories of vision. For the details of these questions reference must be made to the larger text-books of anatomy, physiology, and physiological psychology. A few general works are cited below, together with some special researches to which reference has been made in the preceding text:

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CHAPTER XV

THE OLFACTORY APPARATUS

THE olfactory part of the brain as a whole is sometimes called the rhinencephalon. In fishes (p. 118 and Figs. 43, 44) almost the whole of the cerebral hemisphere is devoted to this function, and as we pass up the scale of animal life more and more non-olfactory centers are added to the hemisphere in the corpus striatum and cerebral cortex, until in man the non-olfactory part of the hemisphere overshadows the rhinencephalon. The complex form of the human cerebral hemisphere cannot be adequately understood apart from a knowledge of this evolutionary history, which has been studied with great care by comparative neurologists. The metamorphosis of the vertebrate cerebral hemisphere from a simple olfactory reflex apparatus in the lower fishes to the great organ of the higher mental processes upon which all human culture depends is a very dramatic history, into which, unfortunately, we cannot here enter.

Smell is evidently the dominant sense in many of the lower vertebrates. That this is the case in the dogfish is shown by the enormous development of the olfactory centers of the brain, to which reference has just been made. And in most of the laboratory mammals, such as the rat and the dog, the sense of smell still plays a very much more important part in the behavior complex than in man and other primates, whose olfactory organs are in a reduced condition.

The *nervus terminalis* is a slender ganglionated nerve found associated with the olfactory nerve in most classes of vertebrates from fishes to man. Its fibers, which are unmyelinated, reach the mucous membrane of the nose, though the precise method of their ending is unknown. They pass inward in company with those of the olfactory nerve as far as the olfactory bulb. Here they separate from the olfactory fibers and enter the cerebral hemisphere between the attachment of the olfactory bulb and the lamina terminalis (Fig. 43, p. 119). Within the brain they have been followed backward in Amphibia through the entire length of the olfactory

area and hypothalamus, but their cerebral connections have never been accurately determined. The function of this nerve is likewise wholly unknown.

In man the terminal nerve is widely distributed to the olfactory mucous membrane of the nose by numerous slender filaments which anastomose freely with each other and are distinct from those of the olfactory nerve with which they are mingled. Numerous ganglion cells are scattered among them, especially in a more densely aggregated ganglion terminale near the olfactory bulb. There are approximately 1500 of these cells on each side of the body. Having entered the cranial cavity, the nervus terminalis passes by the olfactory bulb and extends farther backward, usually in several very slender strands embedded in the pia mater over the gyrus rectus, to enter the brain substance at or near the anterior border of the medial olfactory stria (see Fig. 105). For more complete descriptions see the works of Brookover, Johnston, McCotter, Larsell, and Huber and Guild cited at the end of this chapter.

In the nose of most vertebrates there is a special region containing a portion of the olfactory sensory epithelium known as the vomeronasal organ, or organ of Jacobson. This receives a special slip of the olfactory nerve, the vomeronasal nerve, and in some animals a special accessory olfactory bulb is developed in the brain to receive this nerve (see the papers by McCotter). This apparatus is well developed in the frog and from the accessory olfactory bulb a special olfactory tract is directed into the nucleus amygdalæ in the corpus striatum complex (Herrick, 1921).

The olfactory cerebral centers fall into two groups: (1) the reflex centers of the brain stem and (2) the olfactory cerebral cortex. The arrangements of the olfactory reflex centers and their connecting tracts are essentially similar in plan in all vertebrate brains (except in some aquatic mammals, like the dolphin, which lack olfactory organs altogether). The olfactory cerebral cortex, on the other hand, is very diversely developed in different groups of vertebrates. There is no true cerebral cortex in fishes; in amphibians (particularly in the frog) the olfactory cerebral cortex begins to emerge from the general olfactory reflex centers; in reptiles there is a well-formed olfactory cortex of simple histologic pattern and the beginnings of the non-olfactory cortex; in birds the olfactory apparatus is reduced and the non-olfactory cortex is somewhat more extensive than in reptiles; in mammals both the olfactory cerebral cortex and the non-olfactory cortex attain their maximum dimensions, the former in the lowest members of this group and the latter in the highest.

The cerebral cortex as a whole is sometimes called the *pallium*. That portion of the pallium which is related with the olfactory apparatus was differentiated earlier in vertebrate evo-

lution than the non-olfactory pallium and has, therefore, been called the *archipallium.* The non-olfactory cerebral cortex is termed the *neopallium* (or somatic pallium, for it receives the somatic projection fibers). The archipallium, as already indicated, attains its maximum development in the lowest mammals, particularly the marsupials, like the kangaroo and opossum, consisting of the hippocampus and hippocampal gyrus (gyrus hippocampi, or pyriform lobe). The neopallium attains its maximum size in the human brain, and the indications are that in civilized races it is now in process of further differ-

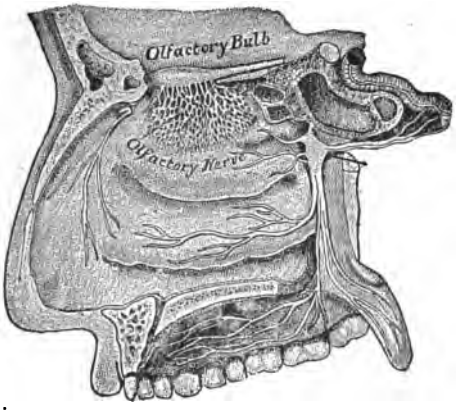

Fig. 103.—Dissection of the right olfactory bulb and nerve on the lateral wall of the nasal cavity. (From Wood's Reference Handbook of the Medical Sciences.)

entiation. In the human brain practically all parts of the exposed cerebral cortex are neopallium, the archipallium being of relatively small size and mostly concealed by a process of infolding along the posterior margin of the neopallium.

In the human body the specific olfactory receptors (see p. 97) are limited to a small area of the mucous lining in the upper part of the nasal cavity on both its lateral (Fig. 103) and its medial walls. The cell bodies of the olfactory neurons of the first order lie in this mucous membrane (Figs. 36 and 104). The axons of these neurons form the fibers of the olfactory nerve, which are unmyelinated; they pierce the ethmoid bone

in numerous small fascicles (fila olfactoria) and terminate by free arborizations in the primary olfactory center within the olfactory bulb (Figs. 53, 103, 104, 106). Several olfactory nerve-fibers terminate together in a dense entanglement of fibers termed a glomerulus, which also receives one or more dendrites from the olfactory neurons of the second order, or mitral cells. The glomerulus, therefore, contains the first synapse in the olfactory pathway. The axons of the mitral cells form the olfactory tract and discharge into the olfactory area, or secondary olfactory nucleus, at the base of the olfactory bulb. These axons give off collateral branches which discharge among very small neurons of the olfactory bulb,

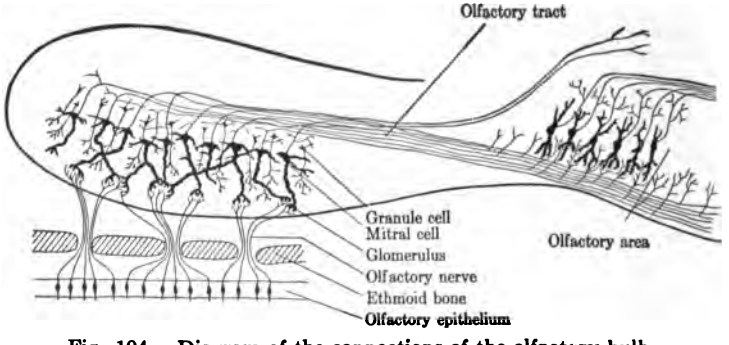

Fig. 104.—Diagram of the connections of the olfactory bulb.

the granule cells, whose chief processes are directed peripheralward, to end among dendrites of the mitral cells.

Attention has already been called (pp. 80 and 97) to the fact that, though smell and taste are both chemically excited senses, the olfactory organs can be excited by much more dilute solutions of the stimulating substances than can the gustatory organs. The lowering of the threshold for olfactory stimuli has been effected by several means, among which we may mention the following: Whereas in the taste-buds there is a synapse between the specific receptor cells and the peripheral nerve-fiber (Fig. 35, p. 96), there is no such synapse in the olfactory organ, the peripheral receptor cell giving rise directly to the olfactory nerve-fiber (Fig. 104). In the second place, the

peripheral gustatory nerve-fiber discharges centrally into several neurons of the primary gustatory center in the medulla oblongata; but many peripheral olfactory fibers enter a single glomerulus, where they are engaged by dendrites from only one or two mitral cells, thus providing for the summation of stimuli in each mitral cell. Again, the collateral discharge from the olfactory tract into the granule cells (which are very numerous) carries the discharge from the mitral cells back again into these cells and thus reinforces their discharge (see pp. 107, 215). By these and other devices exceedingly feeble

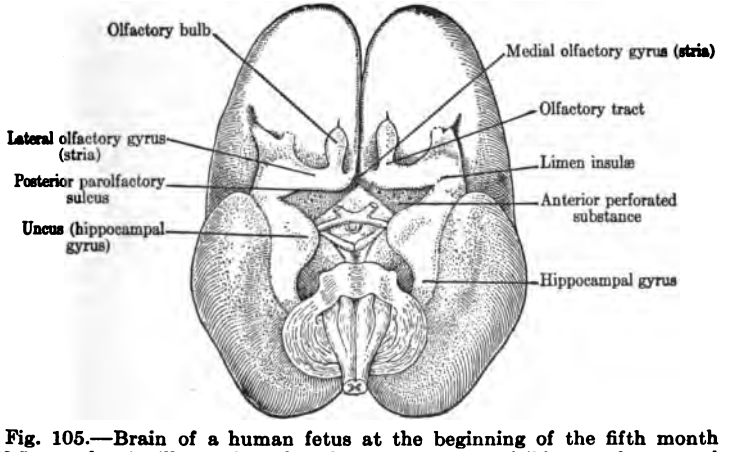

Fig. 105.—Brain of a human fetus at the beginning of the fifth month (22.5 cm. long), illustrating the olfactory centers visible on the ventral surface. (After Retzius, from Morris' Anatomy.)

peripheral stimuli may give rise to very strong excitations in the olfactory centers.

The fibers of the olfactory tract reach the olfactory area, or secondary center, by three paths which spread out from the base of the olfactory bulb and are known as the medial, intermediate, and lateral olfactory striæ (these are shown but not named on Fig. 53, p. 129). The olfactory area has various subdivisions (Fig. 105), the most important of which are: (1) the lateral olfactory nucleus (or gyrus) which receives the lateral olfactory stria and extends backward directly into the

tip of the temporal lobe of the cerebral cortex (uncus), where the ventro-lateral ends of the hippocampus and the hippocampal gyrus come together; (2) the medial olfactory nucleus, including the subcallosal gyrus (Fig. 52, p. 128) and septum, which receive the medial olfactory stria; (3) the intermediate olfactory nucleus, which occupies the anterior perforated substance (Figs. 53, 105) and receives the intermediate ol-

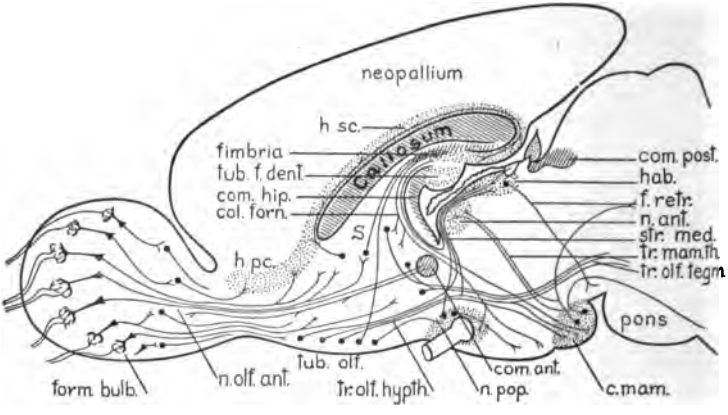

Fig. 106.—Diagram of some of the olfactory tracts in the brain of the rat. The chief connections of the medial and intermediate olfactory tracts are indicated; those of the lateral olfactory tract are omitted: *c.mam.*, corpus mamillare; *col. forn.*, columna fornicis; *com. ant.*, commissura anterior; *com. hip.*, commissura hippocampi; *com. post.*, commissura posterior; *form. bulb.*, formatio bulbaris; *f. retr.*, fasciculus retroflexus of Meynert; *hab.*, habenula, *h.pc.*, hippocampus precommissuralis; *h.sc.*, hippocampus supracommissuralis; *n. ant.*, nucleus anterior thalami; *n. olf. ant.*, nucleus olfactorius anterior; *n. pop.*, nucleus preopticus (ganglion opticum basale); *S*, septum; *str. med.*, stria medullaris thalami; *tr. mam. th.*, tractus mamillo-thalamicus (Vicq d'Azyri); *tr. olf. hypth.*, tractus olfacto-hypothalamicus, or basal olfactory tract; *tr. olf. tegm.*, tractus olfacto-tegmentalis; *tub. f. dent.*, tuberculum fasciæ dentatæ (hippocampus postcommissuralis); *tub. olf.*, tuberculum olfactorium.

factory stria. These nuclei are all important reflex centers, where olfactory stimuli are combined with other sensory impressions, each nucleus having its own particular reflex pattern. The intermediate nucleus (also called tuberculum olfactorium and by Edinger lobus parolfactorius) is better developed in many other mammals than in man, and is

probably especially concerned with the feeding reflexes of the snout or muzzle, including smell, touch, taste, and muscular sensibility, a physiological complex which Edinger has called collectively the "oral sense." This complex of muzzle reflexes has probably played a very important rôle in the earlier stages of the evolutionary history of the correlation centers of the cerebral hemispheres (see the works by Edinger cited at the end of this chapter).

From these nuclei of the olfactory area fiber tracts of the third order pass to the mammillary bodies of the hypothalamus and to the habenular bodies of the epithalamus, from both of which, after another synapse, tracts lead downward into the motor centers of the midbrain in the cerebral peduncle. The path from the mammillary body is the tractus mamillo-peduncularis (Figs. 75, 78, 106). The path from the habenular body is the tractus habenulo-peduncularis (fasciculus retroflexus, B. N. A., or Meynert's bundle, Fig. 106). The mammillary body also sends a tract into the anterior nucleus of the thalamus, the tractus mamillo-thalamicus (fasciculus thalamo-mamillaris, B. N. A., or tract of Vicq d'Azyr, Figs. 78, 106), for the correlation of olfactory with general somatic reactions. There is also a direct path between the secondary olfactory area and the cerebral peduncle, without connection with the diencephalon, by way of the tractus olfacto-tegmentalis (Fig. 106). In the epithalamus the olfactory nervous impulses are correlated with those of the somatic sensory centers of the thalamus, especially the optic and tactual systems (p. 177); in the hypothalamus they are correlated with gustatory and various visceral sensory systems (p. 179).

The preceding account includes a description of a few of the more important pathways involved in olfactory reflexes. Olfactory impulses which reach the cerebral cortex take a different path. They are carried from all parts of the secondary olfactory area at the base of the olfactory bulb into the hippocampus (which composes the greater part of the archipallium in the human brain) by several olfacto-cortical tracts, whose courses in the human brain are so tortuous that we shall not attempt to describe them here.

The hippocampus (formerly called the Ammon's horn or cornu Ammonis, also the hippocampus major, Fig. 107) is a special convolution which forms the postero-ventral border of the cerebral cortex; it is rolled into the posterior horn of the lateral ventricle so that it does not appear on the surface of the brain. It is connected with the remainder of the cortex

Fig. 107.—Section across the hippocampus and gyrus hippocampi of the human brain. (After Edinger.)

(neopallium) by cortex of transitional type, the hippocampal gyrus (gyrus hippocampi), from which it is separated by a deep groove, the fissura hippocampi. The free border of the hippocampus is accompanied for its entire length by a strong

band of fibers, the fimbria, through which olfactory projection fibers enter it from the secondary olfactory area.

The hippocampus is connected with all other parts of the cerebral cortex by an extensive system of association tracts forming the alveus (Fig. 107), thus providing for those complex interactions of diverse functional systems for which the cortex is especially adapted. There is also an efferent pathway from the hippocampus to the brain stem through the fimbria and the column of the fornix (Figs. 78, 106, 107), whose fibers terminate in both the hypothalamus and the epithalamus. Having reached the hypothalamus and epithalamus, these motor impulses of cortical origin are conveyed to the motor centers in the midbrain by the same pathways as are the reflex impulses already described.

Summary.—The olfactory centers (rhinencephalon) make up nearly the entire forebrain in fishes, and in higher vertebrates progressively more non-olfactory centers are added to this part of the brain. The non-olfactory parts of the cerebral hemisphere comprise chiefly the corpus striatum and the neopallium; the latter makes up by far the larger part of the human hemisphere. The rhinencephalon consists of a reflex part in the brain stem and a cortical part in the archipallium. Smell and taste are both chemically excited senses, but the threshold of excitation is much lower in the case of smell. This is brought about by the suppression of a synapse in the peripheral receptor organ and by a complex mechanism for the summation and reinforcement of stimuli in the primary olfactory center in the olfactory bulb. The secondary olfactory center is the olfactory area, which has three parts; each of which is a reflex center of distinctive type. The reflex path from the secondary center passes backward to the epithalamus and to the hypothalamus, from both of which a descending path goes to the motor centers in the cerebral peduncle. The secondary olfactory center also discharges into the olfactory cerebral cortex, which is chiefly contained within the hippocampus and from which manifold association pathways connect with all other parts of the cerebral cortex.

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CHAPTER XVI

THE SYMPATHETIC NERVOUS SYSTEM

BEFORE we can extend our analysis of the conduction paths into the realm of the visceral activities of the body we must consider briefly the sympathetic nervous system through which the regulatory control of these activities is effected. Most of the visceral activities are performed either unconsciously or with very imperfect awareness. The nervous mechanisms of many of them are still obscure. Nevertheless the visceral functions as a whole are of enormous importance, not only in the maintenance of the physical welfare of the body, but also as the organic background of the entire conscious life (see p. 290).

Many of the visceral functions can be performed quite apart from any nervous control whatever by the intrinsic mechanisms of the viscera themselves. The heart musculature, for instance, beats automatically with a characteristic rhythm, and most of the other visceral muscles have the power of automatic rhythmic contraction. Some of the glands of the body may be excited to secretion by chemical substances dissolved in the blood. For instance, when food enters the small intestine from the stomach, the intestinal glands are directly excited to activity by the presence of the food. Some of their secretions are poured out into the intestine to act as digestive juices; others are absorbed directly by the blood (internal secretions or hormones). Among the latter is secretin, a substance which is carried by the blood-stream to the pancreas and there excites the secretory activity of this organ to the formation of pancreatic juice, which is, in turn, poured into the intestine. The very complex secretory activities involved in the formation of the intestinal and pancreatic juices under the stimulus offered by the presence of food in the intestine, therefore, are not directly excited by the nervous system, though they may be brought under nervous control in a

secondary way. And, as a matter of fact, in all of these visceral functions the non-nervous and the nervous functions actually coöperate in most intimate fashion.

Most of the viscera are, accordingly, under immediate nervous control of two sorts. This control is partly derived from the ganglia of the sympathetic nervous system which are distributed widely throughout the body, and partly from the central nervous system. The nervous impulses involved in the second type of control are, moreover, always distributed to the viscera through the sympathetic system.

A clear analytic description of the visceral nervous systems is extremely difficult, and there is wide diversity of usage, not only in the terminology employed in these descriptions, but also in the fundamental concepts upon which they are based. The brain and spinal cord and the cranial and spinal nerves and their end-organs in the aggregate constitute the *cerebro-spinal nervous system.* The cell bodies of the neurons of this system all lie within the spinal cord and brain (including the retina) or in the ganglia on the sensory roots of the cranial and spinal nerves. There are, however innumerable other ganglia distributed very widely throughout the body, which are connected with each other and with the central nervous system by intricate nervous plexuses. These constitute the sympathetic ganglia and nerves, or in the aggregate the *sympathetic nervous system.*

There is an especially important group of sympathetic ganglia which are arranged in two longitudinal series extending one on each side of the vertebral column. These ganglia constitute the vertebral sympathetic trunks or chains, and throughout the middle part of the body there is one ganglion of each trunk for each spinal root (Fig. 41, p. 115). Communicating branches connect the ganglia of the trunks with their respective spinal roots, and from these ganglia sympathetic nerves extend out peripherally to ramify among the viscera and other tissues of the body. Ganglion cells are scattered among these peripheral sympathetic nerves, and in some places, especially among the abdominal viscera, these cells are crowded together to form large ganglionic plexuses (Fig. 108).

When further analyzed, the sympathetic nervous system is

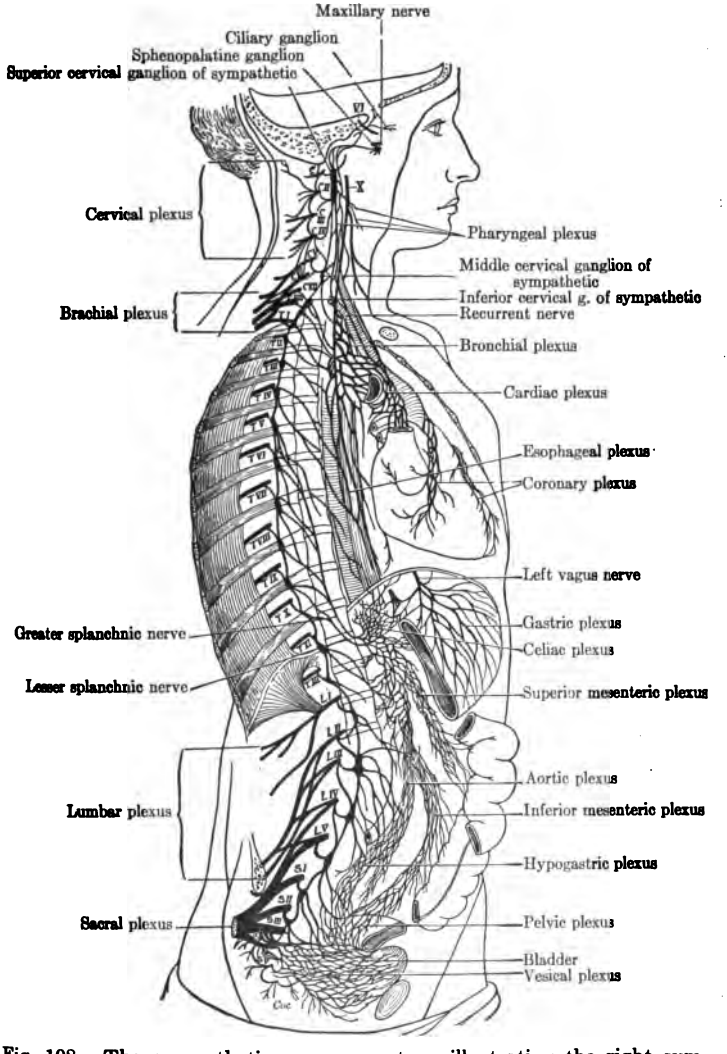

Fig. 108.—The sympathetic nervous system, illustrating the right sympathetic trunk and its relation with the spinal nerves and with the peripheral sympathetic ganglionated plexuses; cf. Fig. 41, p. 115. (After Schwalbe.)

found to consist of two imperfectly separable parts. The first is a diffusely arranged peripheral plexus of nerve-cells and fibers adapted for the local control of the organs with which it is connected. This we shall call the *peripheral autonomous* part of the sympathetic system (this is not the same as the autonomic nervous system of Langley, see p. 260). The second part of the sympathetic system includes those neurons which put the peripheral autonomous system into functional connection with the central nervous system, thus providing a central regulatory control over the autonomous system. This part of the sympathetic nervous system includes the peripheral courses of the neurons involved in the *general cerebro-spinal visceral* reflex systems (see pp. 81, 94, 98).

The peripheral autonomous nervous system appears to be a direct survival of that diffuse type of nervous system which alone is found in the lowest animals which possess nerves at all, such as some jelly-fishes and worms. It serves to supplement the non-nervous protoplasmic activities of the different tissues which coöperate in the performance of the work of the several organs. With increasing complexity of the organization of the body during evolution, protoplasmic activities on the lower physiological level are no longer adequate to effect the integration and coördination of the more diversified functions to be performed in these complex organs. This type of local control is then effected by the peripheral autonomous nervous system.

The central nervous system of higher animals is supposed to have developed by a concentration of ganglia in such a diffuse system (see p. 28), a portion of which remains as the peripheral autonomous sympathetic system (Fig. 17, p. 56). But during further evolution the central nervous system increased in importance for integrating and regulating the functions of the body, the central control of the viscera assumed greater importance, and the general cerebro-spinal visceral systems were developed to serve this function.

That the neurons of the peripheral autonomous system are of more generalized type (and therefore probably more primitive) than are other types of neurons is suggested by the fact that they survive experimental total anemia much longer

than do any other neurons. Cannon and Burket (1913) point out that neurons of the myenteric plexus (p. 270) may survive the anemia caused by ligature of the blood-vessels for as much as 6 or 7 hours. Neurons of the ganglia of the sympathetic trunk (cerebrospinal visceral system) cannot survive more than one hour of this treatment, and those of the spinal cord less than this time, while those of the brain cannot survive more than 15 or 20 minutes.

Figure 56 (p. 136) illustrates the typical arrangement of the visceral sensory and motor fibers in the spinal nerves, and their relations to the sympathetic ganglia and nerves. These fibers, of course, belong to the cerebro-spinal visceral systems; the peripheral autonomous system is not included in the diagram. The central control of the visceral apparatus is effected (1) by afferent visceral nerve-fibers distributed peripherally through the sympathetic nerves and entering the spinal cord through the dorsal spinal roots, and (2) by efferent visceral nerves which leave the spinal cord through the ventral roots and also enter the sympathetic nerves. In lower vertebrates (and possibly also in man) some of these fibers leave by the dorsal roots also.

The cell bodies of the afferent neurons lie in part in the spinal ganglia and in part in the sympathetic ganglia. Figure 109 illustrates the connections of these two types of afferent visceral neurons. Neuron 3 of this figure may transmit its impulse either directly into the spinal cord through its centrally directed process or by a collateral branch to some other cell body of the spinal ganglion (neuron 1). The fiber marked 4 arises from a cell-body lying in some sympathetic ganglion and terminates in synaptic relation with some neuron whose cell body lies in the spinal ganglion, which, in turn, may transmit this visceral impulse into the spinal cord in addition to its own proper function, say, of cutaneous sensibility.

The relations just described probably provide the neurological mechanism of some of the curious phenomena known as referred pains. It is well known that disease of certain internal organs may be accompanied by no pain at the site of the injury, but by cutaneous pain and tenderness in remote parts of the body. Fig. 110 illustrates some of these areas of referred

pain and the sources of the excitations. The mechanisms shown in Fig. 109 show how an inflammatory process or other injury of the sympathetic nerves associated with these deep viscera may readily be carried over to the related neurons of the somatic sensory system. Many referred pains are un-

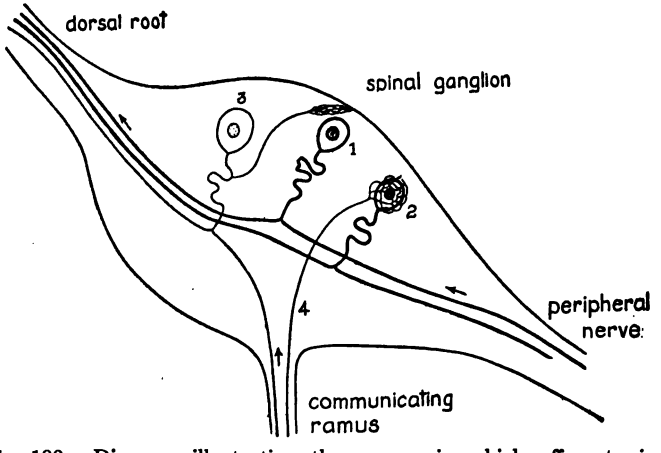

Fig. 109.—Diagram illustrating three ways in which afferent visceral fibers may connect with the central nervous system through the spinal ganglia (cf. Fig. 56, p. 136). Neurons 1 and 2 are typical somatic sensory neurons, whose peripheral fibers reach the skin. Neuron 3 is a visceral sensory neuron, whose peripheral fiber enters the sympathetic nervous system through the communicating branch (this neuron is drawn in fine dotted lines in Fig. 56). Neurons of the third type may bring in afferent impulses from the viscera through their peripheral processes and transmit these impulses directly to the spinal cord through their central processes. A collateral branch from this neuron, moreover, may carry the visceral impulse to the cell body of a neuron of type 1, which thus serves to convey both somatic impulses from the skin and visceral impulses from some deep-seated organ. The spinal ganglion also receives nerve-fibers of the type marked 4, whose cell bodies lie in the sympathetic ganglia. These probably convey visceral afferent impulses as far as the spinal ganglion, which are then transmitted to the spinal cord through a somatic sensory neuron. These arrangements are described in detail by Dogiel, whose account is here followed. It should be added that the presence of visceral afferent neurons of the fourth type is denied by most other students of the question. (See Ranson, 1920.)

doubtedly due to similar collocations of visceral and somatic sensory paths within the spinal cord and brain. Since the functions of these visceral nerves do not usually come into consciousness at all, the pain will be referred to the peripheral

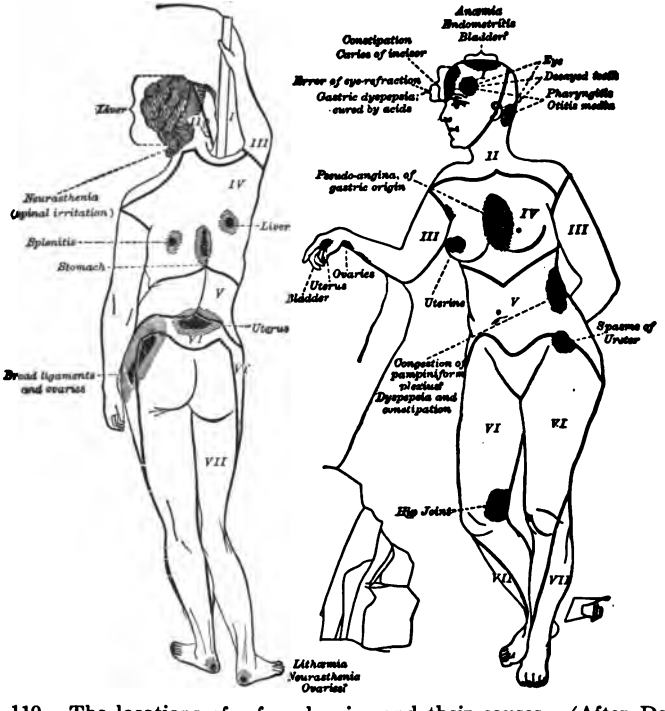

FIG. 110.—The locations of referred pains and their causes. (After Dana, from Starr's Nervous Diseases.)

Area, cerebro-spinal nerves.	*Distribution.*	*Associated ganglia of sympathetic.*	*Distribution.*
I. Trigeminus, facial.	Face and anterior scalp.	Four cerebral.	Head.
II. Upper cervical.	Occiput, neck.	First cervical.	Head, ear.
III. Lower four cervical and first thoracic.	Upper extremity.	Second and third cervical, first thoracic.	Heart.
IV. Upper six thoracic.	Thorax.	First to sixth thoracic.	Lungs.
V. Lower six thoracic.	Abdomen, upper lumbar.	Sixth to twelfth thoracic.	Viscera of abdomen and testes.
VI. Twelfth thoracic and fourth lumbar.	Lumbar, upper gluteal, anterior thigh, and knee.	First to fifth lumbar.	Pelvic organs.
VII. Fifth lumbar and five sacral.	Lower gluteal, posterior thigh and leg.	First to fifth sacral.	Pelvic organs and legs.

area of distribution of the associated somatic nerve, which has a distinct "local sign," or habitual peripheral reference.

The efferent fibers of the cerebro-spinal visceral system arise from several groups of cells in the intermediate zone between the dorsal and ventral gray columns of the spinal cord, and in particular from an intermedio-lateral column of cells at the margin of the lateral column of gray matter (Fig. 56, p. 136). These efferent fibers never reach their peripheral terminations directly. They always end in some sympathetic ganglion, either of the vertebral ganglionic trunk or one of the peripheral sympathetic ganglia. Here there is a synapse, and a second neuron of the sympathetic ganglion in question takes up the nervous impulse and transmits it to its termination in some unstriated visceral muscle or gland. The efferent fiber arising from a cell body within the spinal cord is termed the *preganglionic fiber*, and the peripheral fiber arising from a neuron of the sympathetic ganglion is the *postganglionic fiber*. The former is usually a small myelinated fiber; the latter is usually unmyelinated. The preceding description is applicable to the visceral nervous system in the trunk region of the body. In the head the connections of the nerves of this type are much more complex.

Langley and others have shown that what is here termed the general cerebro-spinal visceral system is related to four distinct regions of the central nervous system, as illustrated by Fig. 111. The portions of the sympathetic system related to these respective regions are as follows: (1) The midbrain sympathetic, comprising chiefly the ciliary ganglion behind the eye and its nerves, these being related to the brain through the III cranial nerve. (2) The bulbar sympathetic, related to the brain chiefly through the VII, IX, and X cranial nerves. (3) The thoracic-lumbar sympathetic, related to the spinal cord through the I thoracic to II or III lumbar nerves. (4) The sacral sympathetic, related to the spinal cord through the II to IV sacral nerves.

Each of these four regions has its own distinctive physiological characteristics, including in some cases a special type of reaction to certain drugs. They all exhibit a common reaction to nicotin in physiological doses. The effect of this poison

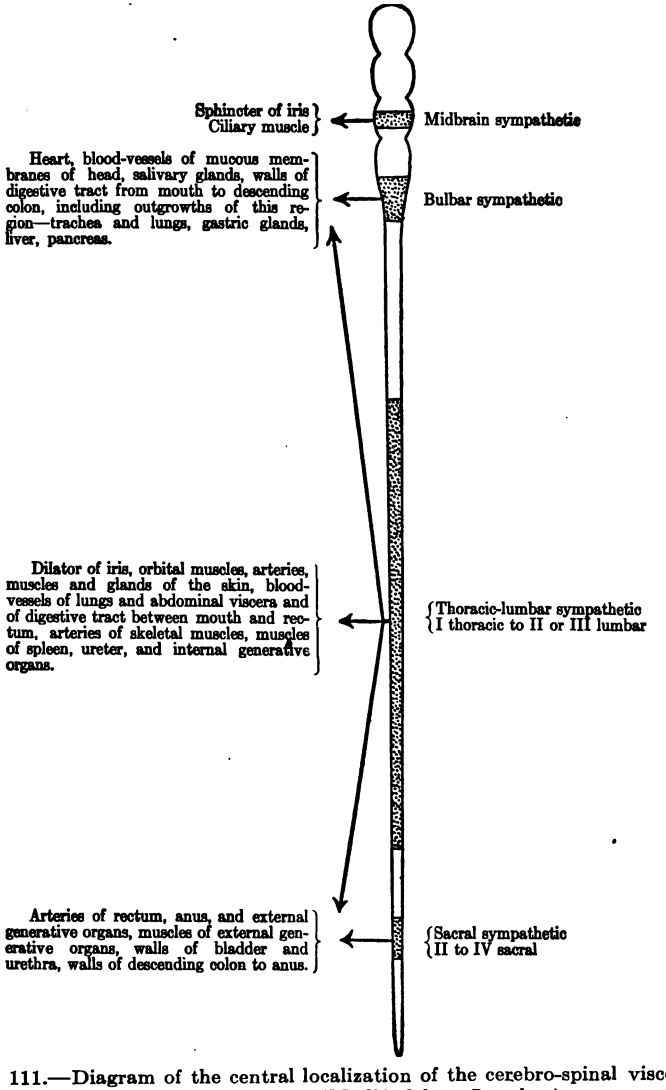

Fig. 111.—Diagram of the central localization of the cerebro-spinal visceral nervous connections. (Modified from Langley.)

is to paralyze the synapses between the preganglionic and the postganglionic neurons and thus to isolate the peripheral sympathetic neurons physiologically from efferent impulses arising within the central nervous system. Adrenalin (extract of the suprarenal glands) affects chiefly the thoracic-lumbar sympathetic system (see p. 285). On the other hand, poisons of a different group, including atropin, muscarin, and pilocarpin, are said to act chiefly upon the midbrain, bulbar and sacral sympathetic, but not upon the thoracic-lumbar system. There are other cases of very specific action of drugs upon special parts of the sympathetic nervous system.

The analysis of the sympathetic nervous system given above differs in some respects from any other in common use. But there is no uniformity in current usage (for a summary of the variations in the nomenclature of the visceral nervous system see Ranson, 1917).

The simplest procedure seems to be to retain the older usage and employ the word sympathetic system as a purely topographic name for that portion of the visceral nervous system which can be dissected away from the cerebro-spinal nerves, viz., the ganglionated trunks and plexuses, together with the whole of what is here termed the peripheral autonomous visceral system, and their related peripheral nerves. The rami communicantes provide the only connection between this system and the spinal cord and spinal nerves; but the relations of the sympathetic system to the cranial nerves is much more complex and the anatomical separation of these two systems here is often impossible.

There is a practical justification in dissecting-room convenience for this usage; but for purposes of finer histological and physiological analysis the distinction between sympathetic and cerebrospinal nerves here drawn must be ignored. The term autonomic nervous system has been used in so diverse senses that it should be abandoned altogether.

Langley calls the entire sympathetic system the autonomic system, and limits the application of the term "sympathetic" to what is here called the thoracic-lumbar sympathetic. There is no adequate ground for his belief that the latter is genetically different from the other parts of the cerebro-spinal visceral apparatus, though its physiological characteristics are very distinctive. Many of the viscera have a double innervation through the sympathetic, one set of fibers coming from the midbrain, bulbar, or sacral sympathetic ganglia and an antagonistic set coming from the thoracic-lumbar sympathetic ganglia.

Summary.—From the preceding considerations it is evident that the sympathetic nervous system cannot be sharply separated anatomically or physiologically from the cerebro-spinal system. The cell bodies of the neurons of the cerebro-spinal visceral system lie partly within and partly without the central

nervous axis. A ganglionic sympathetic trunk extends on each side of the body along the spinal column, and the ganglia of this trunk are connected with most of the spinal nerves by communicating branches. The neurons of this trunk of vertebral sympathetic ganglia belong chiefly to the cerebro-spinal visceral system, since they are concerned with the central regulatory mechanism of the viscera. All parts of the visceral nervous system which lie peripherally of the communicating branches between the sympathetic ganglionated trunks and the spinal roots, and can be anatomically separated from the peripheral branches of the cerebro-spinal nerves, are commonly described as constituting the sympathetic nervous system. This system includes the ganglionated trunks bordering the spinal column, to which reference has just been made, the larger peripheral ganglionated plexuses of the head, thorax, and abdomen, and a very large number of minute sympathetic ganglia scattered everywhere throughout the body. This sympathetic nervous system we have regarded as composed of two imperfectly separable parts: (1) a series of autonomous peripheral ganglia for the local regulation of the organs within which they are found; (2) the neurons of the cerebro-spinal visceral systems which enable the central nervous system to maintain a regulatory control over the intrinsic autonomous systems.

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CHAPTER XVII

THE VISCERAL AND GUSTATORY APPARATUS

Our knowledge of the functional localization within the spinal cord of the general visceral reflex centers related to the spinal nerves is still rather indefinite. Most of the cerebrospinal control of the visceral reactions of the body is effected from the bulbar sympathetic centers by way of the vagus nerve. The afferent fibers of these systems all enter the fasciculus solitarius, a longitudinal bundle of fibers in the lower part of the medulla oblongata, and they terminate in the nucleus of visceral sensory neurons which accompanies this fasciculus (Figs. 71–74, 77, 114). The special visceral fibers of the nerves of taste also terminate in this nucleus. The efferent fibers of these systems arise chiefly from the dorsal motor nucleus of the vagus, a cluster of neurons which produces an eminence in the floor of the fourth ventricle known as the ala cinerea or trigonum vagi (Figs. 71–74, 114). From this nucleus arise preganglionic fibers for the innervation of various systems of visceral muscles of blood-vessels, esophagus, stomach, intestine, bronchi, and others.

Most viscera possess a double innervation—from the thoracic-lumbar sympathetic system and from the midbrain, bulbar, or sacral system (see p. 260). For instance, the heart-beat is accelerated by the thoracic-lumbar system and inhibited by the bulbar system through the vagus; and the iris is contracted through the midbrain sympathetic, but dilated through the thoracic by way of the superior cervical ganglion (p. 237).

Organs of Circulation.—The nervous control of the heart and blood-vessels is far too complex for full description here. A few general features only can be touched upon.

The rate of blood flow may be varied for the body as a whole by changes in the rate and force of the pulsations of the heart, and for particular parts of the body by changes in the caliber

of their blood-vessels. The heart beats automatically, but its rate is regulated through the cardiac nerves. The caliber of the smaller blood-vessels and hence the amount of blood which can pass through them is regulated by vasomotor nerves. Both the heart and the muscular walls of the vessels have a double innervation. The heart has an accelerator nerve and an inhibitory nerve; the smaller arteries have vasodilator and vasoconstrictor nerves. The amount of blood pumped by the heart at any time will depend upon the equilibrium existing between its accelerator and its inhibitory fibers and upon the resistance offered by the peripheral vessels; that flowing through any particular system of blood-vessels will be affected also by the equilibrium between the vasodilator and the vasoconstrictor nerves of these vessels.

There are sympathetic ganglia within the heart. Its extrinsic nerve supply includes afferent fibers to the brain and efferent fibers of two sorts, viz., the accelerator and inhibitory fibers already mentioned. The afferent fibers are represented in a small sympathetic nerve, the nerve of Cyon, which is also called the depressor nerve. They arise from the walls of the ventricles of the heart and join the vagus trunk, through which they enter the medulla oblongata. Stimulation of this nerve produces a fall of arterial pressure by dilating the vessels throughout the body, especially in the viscera. It appears to act to reduce the labor of the heart when intraventricular pressure becomes excessive.

The medulla oblongata contains a center whose stimulation causes inhibition of the heart-beat. These efferent fibers go out as preganglionic fibers of the vagus nerve and terminate in the cardiac sympathetic plexus (Fig. 108), where their post-ganglionic neurons are located. There is also a center in the medulla oblongata (which has not been precisely localized) whose stimulation causes acceleration of the heart-beat. These accelerator nerve-fibers do not leave the brain through the vagus, but apparently they descend through the spinal cord to the lower cervical region and pass out into the sympathetic nervous system at this level. The centers of vasomotor control of various regions of the body are indicated in Fig. 111.

Ranson and von Hess ('15) have given evidence that in the spinal cord of cats the conduction path for pain, for depression of blood pressure and for respiratory changes lies in the dorsal part of the lateral funiculus and that there is a second pathway involving changes in blood pressure in the fasciculus dorso-lateralis (Lissauer's tract) whose stimulation raises the blood pressure.

Ranson and Billingsley ('16) have later shown that the unmyelinated fibers of the dorsal spinal roots are conductors of painful impressions.

Organs of Respiration.—Oxygen is supplied to the tissues of the body in a great variety of ways in different animals. In some of the simpler animals, as in plants generally, oxygen is simply absorbed from the surrounding medium by the exposed surfaces. In all but the lowest animals there is a blood-vascular system by means of which the oxygen absorbed at the surface is transferred to the deeper tissues. In insects, however, this result is obtained chiefly by a different apparatus, namely, a system of air tubes (tracheæ) which ramify among the tissues and supply oxygen directly to the functioning cells. In most water-breathing animals a portion of the surface of the body is lamellated and vascularized to form gills to faciliate the absorption of oxygen by the blood-stream, and in air-breathing vertebrates lungs are developed to accomplish the same result. The nervous mechanisms of respiration will differ in all of the cases cited above, and it is only in mammals that we shall here consider the details of this mechanism.

In ordinary breathing, inspiration is effected by actively increasing the volume of the thoracic cavity and thus creating a suction through the trachea, while expiration is the result of the passive return of the organs involved to their former positions by reason of their own elasticity. The muscles involved in inspiration belong to two groups: (1) the internal apparatus, *i. e.*, the diaphragm, and (2) the external apparatus, the intercostal and other muscles of the body wall. These are all somatic muscles. In forced respiration various other muscles act in an accessory way during both inspiration and expiration.

The diaphragm is innervated by the phrenic nerve, which takes its origin from the fourth and fifth cervical spinal nerves; and the intercostal muscles are innervated by ventral spinal roots arising successively from all thoracic segments of the

spinal cord (Fig. 112). The accessory muscles are in part somatic muscles of the abdomen and shoulder and in part special visceral muscles of the head, particularly those of the glottis (innervated by the vagus) and of the nostrils (innervated by the VII cranial nerve).

The anatomical relations just described imply that, although respiration is a visceral function, in mammals the necessary

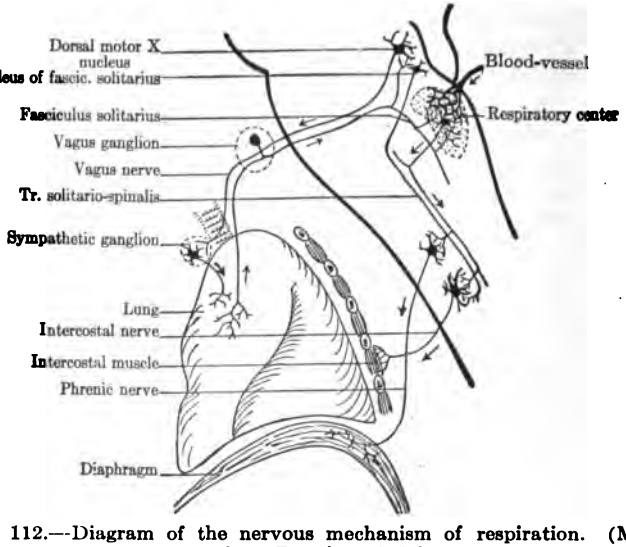

Fig. 112.—Diagram of the nervous mechanism of respiration. (Modified from Ramón y Cajal.)

movements for ordinary breathing are performed by somatic muscles. This is not true in fishes. Here the organs of respiration (gills) are strictly visceral structures innervated by visceral components of the cranial nerves, whose cerebral center is in the lower part of the medulla oblongata (the visceral sensory area of Fig. 68, p. 166).

In the ordinary breathing of mammals the act of inspiration is effected by an upward and outward movement of the ribs and a downward movement of the diaphragm. Now, if the spinal cord be cut through at the level of the seventh cervical nerve the respiratory movement of the ribs is entirely abolished, though the movements of the diaphragm go on as usual. The

continuity of the thoracic motor nerves which innervate the intercostal muscles with their centers of origin in the spinal cord is undisturbed by this operation, yet they can no longer be coördinated in the respiratory act. If in another animal the spinal cord be divided at the level of the third cervical nerve, *i. e.*, above the level of origin of the phrenic nerve, the respiratory movements of both the ribs and the diaphragm cease, even though the spinal cord below the section is intact and its connection with the peripheral respiratory apparatus is undisturbed. These experiments show that the spinal segments from which all of the motor respiratory nerves arise cannot of themselves effect the coördinations necessary in respiration. This is in marked contrast with many other reactions (both visceral and somatic), whose performance is still possible after the separation of the spinal cord from the brain.

If now, in a third animal, the medulla oblongata is cut across at any point above the middle of its length, say at the lower border of the pons, the respiratory processes are in no way disturbed. This shows that there is a respiratory correlation center in the lower half of the medulla oblongata, that is, somewhere in the region corresponding to the "visceral area" of the fish brain.

The air tubes of the lungs are provided with smooth muscle-fibers by which their caliber may be contracted. These muscles are innervated by the vagus (Larsell), and the hyperexcitation of their motor nerves may impede respiration, this being one of the factors which cause asthma. The cerebral center from which these intrinsic muscles of the lungs are innervated has been shown to lie in the middle part of the dorsal motor vagus nucleus (Fig. 73, *nuc. dorsalis vagi*). These are preganglionic neurons, the corresponding postganglionic neurons lying in sympathetic ganglia distributed along the pulmonary branches of the vagus (Fig. 112).

The apparatus described in the preceding paragraph is, however, not responsible for the maintenance of the regular rhythm of breathing. Physiological experiments show that there is somewhere in the lower part of the medulla oblongata a respiratory center which performs this function. This center may be excited to activity directly by variations in the compo-

sition of the blood which reaches it, and particularly by variations in the proportions of carbon dioxid. Its activity may also be modified by nervous influences reaching it through the peripheral afferent nerves, the vagus being the only nerve which appears to be able to act directly on the respiratory center, though the strong excitation of almost any sensory nerve of the body may under some circumstances indirectly affect the respiratory rhythm. Coughing and sneezing are special cases of this sort. The reflex mechanism of the cough is illustrated in Fig. 113.

Attempts to localize the respiratory center in the mammalian medulla oblongata more accurately have led to contradictory results. The old conception of Flourens that there is a minute "vital node" under the lowest point of the fourth ventricle which is the respiratory center must be abandoned. Later the fasciculus solitarius was identified as the "respiratory tract," and the nucleus associated with this tract was regarded as the respiratory center, but further experiment has shown that this is not an exact statement of the case. Some physiological experiments have suggested that the respiratory rhythm is maintained by a center in the reticular formation of the vagus region ventrally of the fasciculus solitarius.

It has recently been shown, as stated above, that afferent visceral fibers from the lungs whose cell bodies lie in the vagus ganglion enter the fasciculus solitarius, and it is known that from the nucleus of this tract a "tractus solitario-spinalis" (Fig. 112) descends into the motor centers of the upper segments of the spinal cord. This descending visceral spinal tract probably plays some part in the regulation of respiration, though not the chief rôle. Ramón y Cajal and Kappers believe that, while the upper part of the nucleus of the fasciculus solitarius has nothing to do with respiration, the lower end of this nucleus (commissural nucleus of Cajal, see Figs. 71, 112, and 114) is a true respiratory center. Ramón y Cajal, in fact, thinks that this nucleus serves both for reflexes excited by the sensory pulmonary nerves and also for the normal respiratory rhythm excited by carbon dioxid in the blood. This hypothesis is not supported by direct physiological experiment, and for the present we must content ourselves with the statement that the true respiratory center has not been accurately located anatomically. Figure 112 may be regarded as a true picture of the essential relations of the respiratory nerves, with the reservation that the position of the respiratory center is not precisely known.

There is also a reflex center for the regulation of respiration in the medial wall of the thalamus and others have been described in different parts of the brain stem. The entire respiratory mechanism is also under partial voluntary control from the cerebral cortex.

While many features of the central respiratory mechanism remain obscure, it seems evident that the location of the chief respiratory center in the "visceral area" of the lower part of the medulla oblongata instead of the portions of the spinal cord

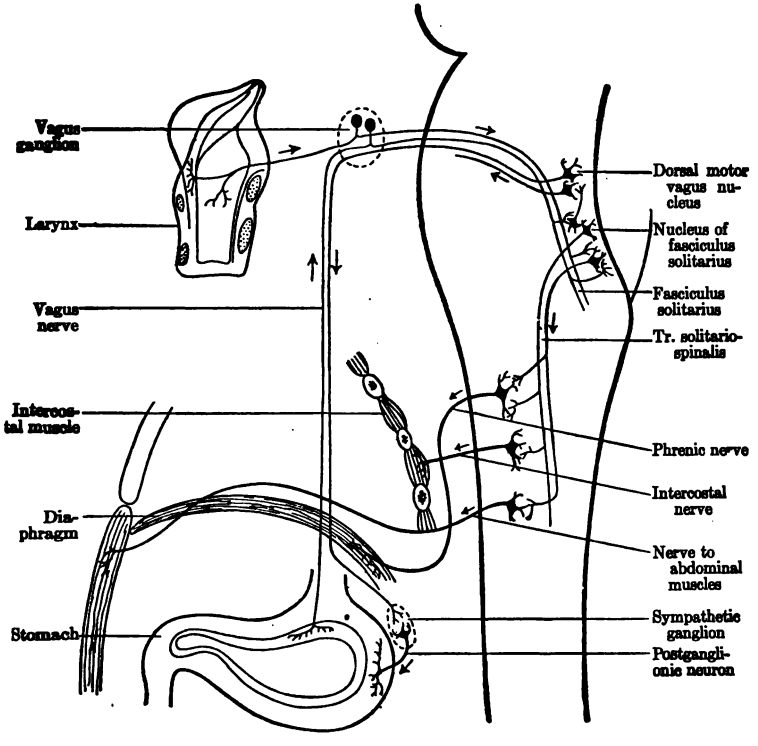

Fig. 113.—Diagram of the nervous mechanisms of coughing and vomiting. In the cough an irritation of the mucous membrane of the larynx is transmitted to the nucleus of the fasciculus solitarius, from which the tractus solitario-spinalis passes downward to the motor centers of the spinal cord for the innervation of the muscles of the diaphragm, the abdominal wall, and the ribs which coöperate in the production of the cough. In vomiting, an irritation of the stomach is carried by sensory fibers of the vagus to the nucleus of the fasciculus solitarius, from which the pathway is as before to the spinal motor centers for the innervation of the diaphragm and abdominal wall. In this case there is also an excitation of the dorsal motor vagus nucleus, from which preganglionic fibers go out into the vagus nerve for a sympathetic ganglion in the gastric plexuses, from which, in turn, postganglionic fibers pass to the muscles of the stomach which participate in the ejection of its contents. The diagram is suggested by one in Ramón y Cajal's text-book, though greatly modified.

directly connected with the respiratory muscles is a survival of the ancestral condition found in fishes, where the entire respiratory function is carried on by a visceral apparatus (gills) innervated from the vagus region.

Organs of Digestion.—Hunger seems to be a complex in which at least three factors are present: (1) Specific hunger pangs due to waves of muscular contraction in the stomach (Cannon, Carlson); (2) appetite, or craving for food regardless of the state of the stomach; (3) general malaise from starvation of the tissues and weakness. Appetite may persist after section of the vagus nerves and is probably a sensation distinct from the hunger pangs.

The ordinary processes of digestion are carried on partly by automatic activities of the organs without nervous control (see p. 251), and partly by the intrinsic sympathetic nervous system of the digestive organs. Throughout the length of the digestive tract there are two sympathetic ganglionated plexuses. One of these is located between the muscular coats of the stomach and intestine, known as the myenteric or Auerbach's plexus; the other lies immediately under the lining mucous membrane and is known as the submucous or Meissner's plexus. It has been shown physiologically that the local reflexes concerned in the typical peristaltic contractions of the digestive tube are effected chiefly by the myenteric plexus. Accordingly, this reflex is called by Cannon the myenteric reflex.

The entire digestive mechanism (like most of the other visceral systems) may also be influenced indirectly by nervous impulses arising in the cerebral cortex, though these organs are not under direct voluntary control. It is well known that the digestive processes are especially sensitive to emotional states, pleasurable experiences promoting digestion and painful or disagreeable emotions inhibiting it. These facts can be studied on laboratory animals under experimental conditions (Cannon). A large amount of information regarding the physiology of digestion has recently been gathered by Carlson from the study of a man with an artificial opening into the stomach (gastric fistula), permitting direct observation of the stomach at all times.

The salivary glands are excited to secretion from two nuclei of the medulla oblongata, the superior salivatory nucleus (Figs.

71, 114), whose preganglionic fibers go out with the VII cranial nerve for the sublingual and submaxillary salivary glands, and the inferior salivatory nucleus (Figs. 71, 73, 114), whose fibers go out with the IX nerve for the parotid gland. The secretion of saliva may be produced either as a simple reflex from the presence of food in the mouth through the gustatory nerves and fasciculus solitarius, or as so-called psychic secretion excited by the sight or thought of food. All of the digestive secretions are susceptible to this sort of indirect excitation, as, indeed, are most other processes which are under the control of the cerebrospinal visceral nervous system. These visceral reactions, in their turn, are reported back to the central nervous system and no doubt play a very large part in shaping the organic background of the entire conscious life (see p. 290).

Students of animal behavior are in the habit of investigating the ability of animals to make simple associations by training them to perform particular acts under conditions such that the normal stimulus to the act is always accompanied by a second stimulus of a different type. After many repetitions the response may be obtained by presenting the second or collateral stimulus without the first. For the nervous mechanism of "associative memory" of this sort see p. 67. Pawlow has found that variations in the amount of saliva secreted form an especially good index of associations of this type, and he has used this method extensively in analyzing complex reactions, or conditional reflexes, as he calls them. See the summary of his researches in the paper by Morgulis cited in the appended bibliography.

Tactile sensibility is entirely absent throughout the entire alimentary canal from the esophagus to the rectum, and the same holds true for most of the other deep-seated viscera of the body. Even the substance of the brain is insensitive to any kind of mechanical irritation. Sensibility to changes in temperature is feebly developed or absent in most of the viscera, the esophagus and anal canal being very sensitive to heat and cold, while the stomach and colon are feebly sensitive to these stimuli. The entire alimentary canal is insensitive to hydrochloric and organic acids in concentrations far in excess of what ordinarily occurs in either normal or pathological conditions. The contact of alcohol with all parts of the mucous

membrane of the alimentary canal gives rise to a sensation of warmth. This sensation is different in character from that caused by hot fluids and is probably excited through the sympathetic nerves, while the sensation of warmth felt in consequence of the passage of hot fluid through the esophagus is excited through the vagus.

The demonstrated absence of tactile sensibility throughout the mucous membrane of the stomach and intestine is considered by Hertz to indicate that the sensations of fulness arising from the distention of different parts of the alimentary canal are due to the stretching of the muscular coat, and that, therefore, these are to be regarded as varieties of the muscle sense. The same may also be true of the bladder. The free nerve-endings (see Fig. 33, p. 95) known to be present in these mucous membranes, particularly in the bladder, may, however, share in exciting these sensations, for these membranes may well be sensitive to stretching, even though quite insensitive to simple pressure. The only immediate cause of true visceral pain is tension, and it is stated by Hertz that, so far as the alimentary canal is concerned, this tension is exerted on the muscular coat, not on the mucous lining.

The swallowing reflex has been restudied by Miller and Sherrington. It may easily be excited in cats by pressure on the back part of the roof of the pharynx, by liquid introduced over the extreme posterior part of the tongue, and by electric stimulation of the fovea inferior in the floor of the fourth ventricle. The cerebral correlation center of this reflex appears to be in the nucleus of the fasciculus solitarius immediately beneath the fovea inferior.

The vomiting reflex may be caused by excitations of sensory termini of the vagus nerve in the stomach, which are transmitted to the nucleus of the fasciculus solitarius in the medulla oblongata, whence the nervous impulses are distributed as shown in Fig. 113 to the appropriate motor centers.

The Gustatory Apparatus.—Taste, like smell, is a chemical sense (see pp. 80, 96, 244). Physiologically, it is classed by Sherrington as an interoceptive or visceral sense, and its primary cerebral center is intimately joined to the general visceral sensory center in the nucleus of the fasciculus solitarius. Unlike the general visceral sensory system, however,

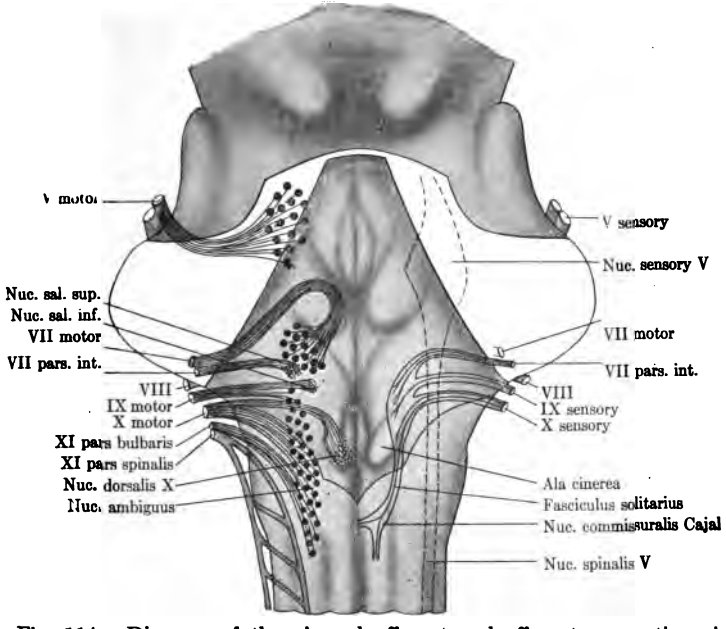

Fig. 114.—Diagram of the visceral afferent and efferent connections in the medulla oblongata, based on Fig. 71; compare also Figs. 77 and 86. The afferent roots and centers are indicated on the right side; the efferent, on the left. Visceral sensory fibers enter by the VII nerve (pars intermedia of Wrisberg, *VII pars. int.*) and by the IX and X nerves. These root-fibers include both general visceral sensory and gustatory fibers, all of which enter the fasciculus solitarius. (Fibers of the IX and X nerves also enter the spinal V tract; but since these are somatic sensory fibers from the auricular branch they are not included in the diagram. For further details on the composition of these cranial nerves see the table on pp. 160, 161.)

On the left side of the figure the general visceral efferent nuclei are indicated by small dots and the special visceral nuclei by large dots. The latter comprise the motor V nucleus for the jaw muscles, the motor VII nucleus for the muscles related to the hyoid bone and the general facial musculature, and the nucleus ambiguus supplying striated muscles of the pharynx and larynx by way of the IX and X nerves. Three general visceral efferent nuclei are indicated—the dorsal motor nucleus of the vagus under the ala cinerea and the superior and inferior salivatory nuclei. The superior nucleus (*nuc. sal. sup.*) supplies the sublingual and submaxillary salivary glands by way of the VII nerve (pars intermedia of Wrisberg), and the inferior nucleus (*nuc. sal. inf.*) supplies the parotid salivary gland by way of the IX nerve. All of the general visceral efferent fibers are preganglionic sympathetic fibers (see p. 258) which end in sympathetic ganglia, whence postganglionic fibers carry the nervous impulses onward to their respective destinations.

its peripheral fibers have no connection with the sympathetic nervous system and the reactions may be vividly conscious. The end-organs, or taste-buds (Fig. 35, p. 96), are present in the mucous membrane of the tongue, soft palate, and pharynx and are innervated by the VII and IX cranial nerves; there are a few taste-buds also on the larynx and epiglottis which are probably supplied by the vagus (J. G. Wilson). All of these peripheral gustatory fibers, upon entering the medulla oblon-

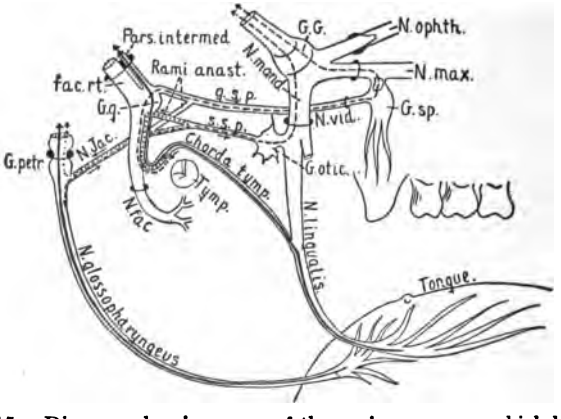

Fig. 115.—Diagram showing some of the various courses which have been advocated for the taste fibers in man. The courses advocated in this work are shown by heavy black lines; other suggested courses are indicated by broken or dotted lines: *fac. rt.*, motor facial root; *G.G.*, Gasserian ganglion; *G.g.*, geniculate ganglion; *G. otic*, otic ganglion; *G. petr.*, ganglion petrosum; *G. sp.*, sphenopalatine ganglion; *g. s. p.*, great superficial petrosal nerve; *N. fac.*, facial trunk; *N. Jac.*, Jacobson's or the tympanic nerve; *N. vid.*, vidian nerve; *Rami anast.*, anastomotic rami between the geniculate ganglion and tympanic plexus and the small and great superficial petrosal nerves respectively; *s. s. p.*, small superficial petrosal nerve; *Tymp.*, tympanum. (After Cushing.)

gata, terminate in the nucleus of the fasciculus solitarius (Figs. 71, 72, 73, 114) along with those of general visceral sensibility, those of the gustatory system probably ending farther forward (toward the mouth) in this nucleus than those of the general visceral systems.

There has been considerable controversy as to the exact course taken by the peripheral nerves of taste on their way to the brain, many clinical neurologists believing that all of these

fibers enter the medulla oblongata through the root of the V cranial nerve. It has now been clearly shown by the studies of Cushing and others that the V nerve takes no part in the innervation of taste-buds. Figure 115 shows in continuous lines the true courses of the nerve-fibers from the taste-buds of the tongue through the VII and IX nerves, and in broken and dotted lines some of the other courses which have been suggested.

In fishes the gustatory system is much more extensively developed than in mammals, especially the vagal part which supplies taste-buds in the gill region. In some species of fishes, moreover, taste-buds appear in great

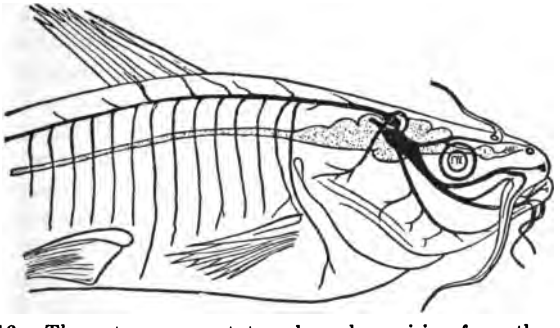

Fig. 116.—The cutaneous gustatory branches arising from the geniculate ganglion of the facial nerve of the catfish (*Ameiurus melas*), projected upon the right side of the body. Spinal cord and brain stippled. The geniculate ganglion, its roots and cutaneous branches are drawn in black; the branches of this nerve distributed to the mucous lining of the mouth cavity are omitted, Taste-buds are found in all parts of the outer skin to which these branches are distributed.

numbers in the outer skin, and these are in all cases innervated from the VII cranial nerve. In the common horned-pouts or catfishes and in the carps and suckers these cutaneous taste-buds are distributed over practically the entire body surface, and especially on the barblets. The distribution of these cutaneous gustatory branches of the facial nerve in the common bullpout, Ameiurus, is shown in Fig. 116. These sense-organs and their nerves are entirely independent of those of the lateral line sensory system and of the ordinary tactile system, though the gustatory and the tactile systems have been shown experimentally to coöperate in the selection of food. The primary terminal nuclei of these gustatory nerves make up by far the larger part of the visceral area (Fig. 68, p. 166) of fish brains, and in some species these centers are enormously enlarged, as in the carp (Fig. 139 (2), p. 340).

The primary sensory center for the nerves of taste in the nucleus of the fasciculus solitarius is very intimately connected with all of the motor centers of the medulla oblongata for the reactions of mastication and swallowing, and also with the motor centers of the spinal cord. The ascending path from the primary gustatory nucleus to the thalamus and cerebral cortex is not fully known in the human body (p. 172). A gustatory center is believed to exist in the cortex of the gyrus hippocampi near the anterior end of the temporal lobe. In fishes, where this ascending gustatory path is much larger, it has been followed to the roof of the midbrain and, after a synapse here, to the region of the hypothalamus (Herrick, 1903, 1905, 1908).

Visceral Efferent Centers.—The arrangement of the visceral efferent nuclei and nerve-roots of the medulla oblongata is shown in Fig. 114. There is also a general visceral efferent component of the III cranial nerve (Fig. 71, p. 168, *nuc. III. E-W.*), whose fibers pass out through this nerve to the ciliary ganglion in the orbit, which in turn connects with the intrinsic muscles of the eyeball in the ciliary process and iris. These fibers are involved in the movements of accommodation of the eye for varying distances and in the regulation of the diameter of the pupil. The nucleus of the fasciculus solitarius is connected through the reticular formation with all of the motor centers of the medulla oblongata for the reactions of mastication and swallowing and for many other movements; from this nucleus there is a descending tract to the motor centers of the spinal cord, the tractus solitario-spinalis (Figs. 112 and 113). There is also a connection with the superior and inferior salivatory nuclei of the VII and IX nerves. The excitation of the gustatory fibers of these nerves by the presence of food in the mouth is carried to the nucleus of the fasciculus solitarius and thence through the reticular formation to the salivatory nuclei, from which the flow of saliva is excited. There are other connections with the motor centers of the spinal cord through the descending fibers of the fasciculus solitarius, some of these fibers crossing to the opposite side in the vicinity of the commissural nucleus of Cajal (Fig. 114).

Summary.—The cerebro-spinal visceral systems fall into a general group related peripherally to the sympathetic nerves

and a special group independent of the sympathetic. The second group includes the apparatus for taste and probably for smell. The central innervation of the viscera is partly from the spinal and midbrain regions, but chiefly from the visceral area of the medulla oblongata. The heart and blood-vessels have a double innervation derived from both the spinal and the bulbar visceral centers, and the nervous control of the organs of circulation is very complex. Respiration in lower vertebrates is effected by strictly visceral structures and is controlled from the visceral area of the medulla oblongata. In mammals the muscles of ordinary respiration are all of the somatic type, but the centers of control are retained in the visceral area of the oblongata. The sensations related to the digestive tract are served chiefly (though not exclusively) by the vagus. There are special salivatory nuclei related to the VII and IX cranial nerves. The nerves of taste are the VII, IX, and to a very limited extent (in man) the X pairs of cranial nerves. The primary cerebral gustatory center is in the upper part of the nucleus of the fasciculus solitarius, but the cortical path is unknown.

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CHAPTER XVIII

PAIN AND PLEASURE

FEW problems in neurology are more difficult and involved than those centering about the nerves of painful sensibility. This question is intimately related with the disagreeable and pleasurable feelings and with the affective and emotional life as a whole. Nearly all sensations, whether of the somatic or visceral series, appear to have an agreeable or disagreeable quality (quale). There is difference of opinion as to whether any sensation is wholly indifferent in this respect. There are, however, two factors in this situation which have not always been distinguished and whose introspective analysis is very difficult. In the first place, many sensations are as such painful or pleasurable, and in the second place the related apperceptions, ideas, etc., may have an agreeable or disagreeable feeling tone. The intimate relation of these two factors in consciousness probably grows out of a similarity in the type of physiological process involved in their neurological mechanisms, and this, in turn, may rest on the fact that the two mechanisms in question have had a common evolutionary origin.

The stimulation of some of the sense organs results in the so-called sensation of pain with no other quality recognizable; this is true of the cornea, of the tooth pulps, of the tympanic membrane, and of the "pain spots" of the outer skin. This fact would suggest that there is a special system of neurons (or at least of receptors, see p. 91) for pain as for the other senses. But, on the other hand, the supernormal stimulation of most other sense organs may result in a very similar type of pain, though in this case the painful quality is accompanied by the normal sensory quality of the organ in question unless the stimulation is excessively strong. From this it would appear that most sensory nerves may upon occasion function as pain nerves. In other cases normal stimulation of a sense organ

may result in a sensation of the quality typical for the organ in question, to which there is added an agreeable or disagreeable quality which may be very pronounced, the disagreeable quality not being painful in the ordinary sense of that term. This mixed quality of normal sensations is illustrated by certain odors and savors, and on the agreeable side by certain sensations of tickle and warmth. Finally, some ideational processes have an agreeable or disagreeable quality, and these, in turn, are very intimately related with the emotions and with esthetic and appreciative functions of the most complex psychic sort, as well as with questions of habitual emotional attitude and temperament.

The superficial parts of the body which are more directly exposed to traumatic injury are, in general, more sensitive to pain than are the deeper parts, and painful stimuli here can be more accurately localized. In some parts, like the conjunctiva of the eyeball, where very slight irritation may seriously interfere with the function, very gentle stimulation gives rise to acute pain, and no other sensory quality may be present.

Surgeons find that the brain membranes are sensitive to mechanical injury, especially to stretching or pulling. The brain substance itself, however, is quite insensitive to pain from either mechanical or chemical stimulation. The deeper viscera of the thorax and abdomen are insensitive to pinching, cutting with a sharp instrument, or other mechanical, chemical, or thermal stimuli, though they are sensitive to pains arising from internal disorders, as in colic (p. 272). The visceral pains are of a very peculiar sort, and are probably in most cases due to muscular tensions. Only on the parietal portions of the pleural and peritoneal membranes can painful stimuli be accurately localized.

From these considerations it appears that pain is an adaptive function which is present only where it is of value to give warning of noxious influences liable to injure the body unless removed. (See the excellent discussion by Sherrington in Schäfer's Physiology, vol. ii, pp. 965–1001.)

Pains of this sort are physiologically similar to other exteroceptive sensations, that is, they have a definite localization and are externally projected like other somatic sensations. But

other pains and discomforts (especially those related to the visceral functions) and all pleasurable feelings are devoid of this external projicience and are experienced merely as a non-localized awareness of malaise or well-being (see p. 290). They are also more variable in relation to habit, mental attitude, fatigue, and general health. This latter group of affective processes is so different from the ordinary sensations as to make it desirable to consider them separately, and, as will appear beyond, they probably involve a quite different series of nervous processes.

There has been much controversy regarding the pathway taken by painful impulses through the spinal cord and brain stem, and it is probable that this pathway is very complex. All painful impulses carried by the spinal nerves, no matter what the peripheral source, are discharged immediately upon entering the spinal cord into its gray matter, and after a synapse here the nerve-fibers of the second order seem to take several courses. The recent experiments of Karplus and Kreidl (1914) go to show that the ascending impulses of painful sensibility in the spinal cord of cats follow a chain of short neurons, some of whose axons immediately cross to the opposite side of the cord and some ascend on the same side. These short fibers belong to the fasciculus proprius system (p. 137), and the nervous impulse is at frequent intervals returned to the gray matter to pass from one neuron to another, and it may cross the midplane repeatedly. This diffuse method of conduction appears to be the primitive arrangement. In the human spinal cord it is probably present to a limited extent, but has been largely supplanted by a more direct pathway in the spinal lemniscus, whose precise localization has been determined by the clinical studies of Henry Head and others (pp. 150, 189). This direct path for fibers of painful sensibility includes axons of neurons of the dorsal gray column, which immediately cross to the opposite side of the cord and ascend directly to the thalamus. Injury to this path in the human body may cause complete insensitivity to both superficial and deep pain on the opposite side of the body below the site of the injury, without loss of general tactile sensibility. The two methods of transmission of impulses of painful sensibility are shown diagrammatically in Fig. 117.

It may be assumed that pain and an avoiding reaction and pleasure and a seeking reaction have come to be instinctively associated by natural selection or other biological agencies because this is an adaptation useful to the organism. No separate neurons would be required for the transmission and analysis of painful stimuli in their simpler forms. A peripheral neuron, say, of the pressure sense, if excited by the optimum stimulus will transmit the appropriate nervous impulse to the tactile centers of the thalamus and cerebral cortex. But the peripheral sensory neurons branch widely within the spinal cord and there effect very di-

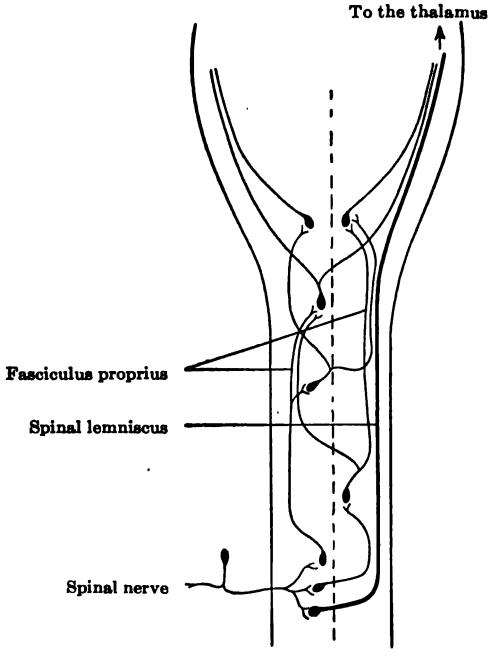

Fig. 117.—Diagram of the pathways of painful sensibility in the spinal cord. The spinal lemniscus is the dominant path in the human body, and the fasciculus proprius is the dominant path in other mammals.

verse types of connection (see Fig. 61, p. 144); and supernormal or maximal stimulation of the end-organ may excite so strong a nervous discharge as to overflow the tactile pathway in the spinal cord by overcoming the synaptic resistance of certain other collateral pathways with a higher threshold than those of the tactile path, thus exciting to function the pathway for painful sensibility with its own central connection in the thalamus (Fig. 118, A).

In the course of the further differentiation of the cutaneous receptors,

the peripheral fiber of the sensory neuron may branch and effect connection with two types of sense organs, one organ (a tactile spot) with a low threshold for pressure stimuli whose nervous impulses are so attuned as to discharge centrally at the first synapse into the tactile tract, and another organ differently constructed (a pain spot) which generates nervous impulses so attuned as to discharge centrally into the pain tract (Fig. 118, B). In a still more highly elaborated system two separate peripheral neurons may be present to serve these functions, which are distinct throughout (Fig. 118, C). The experiments of Ranson (see p. 265) seem to indicate that in cats the fibers of the peripheral nerve roots which conduct painful sensibility are distinct, as illustrated in this third case, and that centrally these fibers (which are unmyelinated) form a special tract in the fasciculus dorso-lateralis (Lissauer's tract) and terminate in the gelatinous substance of Rolando (see Fig. 58, p. 139). Some clinical cases suggest that pain from external pressure may be carried in by sympathetic nerves (p. 197).

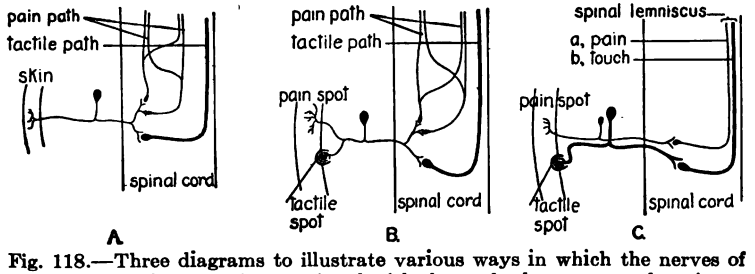

Fig. 118.—Three diagrams to illustrate various ways in which the nerves of painful sensibility may be associated with those of other sensory functions.

All three of these methods of pain transmission and analysis may be present in the spinal nerves; but by whatever pathway the pain impulses reach the spinal cord, in the human body those which are destined to excite consciousness of pain as a localizable sensation are immediately filtered off from the other sensory qualities with which they may be associated and assembled in a pathway of their own, which remains distinct from this time forth. Within the spinal cord and brain stem these pain impulses, especially those resulting from supernormal stimulation, also effect short reflex connections with the adjacent motor centers for quick avoiding reflexes, and these may not be associated with the spinal lemniscus, but with the more diffuse pain path in the fasciculus proprius.

The terminus of the ascending pain tract is related within the thalamus very differently from those of the pathways for tactile and thermal sensitivity. The latter impulses are in part transmitted to the motor centers of the thalamus for intrinsic thalamic reflexes, but chiefly pass forward after a synapse in the thalamus through the internal capsule to the somesthetic centers of the cerebral cortex. Head is of the opinion that the painful impulses do not reach the cortex at all in their

simple elementary form, but that the painful sensations are essentially thalamic (cf. p. 182).

Lesions of the lateral and ventral nuclei of the thalamus involving the termini of the medial lemniscus, but leaving the geniculate bodies and pulvinar and the medial and anterior nuclei intact, result in the more or less complete loss of superficial sensation of the opposite side of the body, with still more profound disturbance of deep sensibility and the postural sensations, together with an exaggeration of painful sensibility. The modifications of pain and affective sensibility are regarded by Head and Holmes as the most constant and characteristic features of lesions of the lateral zone of the thalamus. Acute, persistent, paroxysmal pains are always present, often intolerable and yielding to no analgesic treatment. There is also a tendency to react excessively to unpleasant stimuli. This is not necessarily associated with a lowering of the threshold of stimulation. Deep pressure is especially important here. The pain does not develop gradually out of the general sensation, but appears explosively. This pain has some factors to which the normal half of the body is not particularly susceptible. Thermal, visceral, and other sense qualities are similarly affected. Tickling is very unpleasant on the affected side. The pleasurable aspect of moderate heat is accentuated on the affected side, yet the threshold for heat is never lowered. Not only does the side of the body involved react more vigorously to an affective element of a stimulus, but an overreaction can also be evoked by purely mental states. The manifestations of this increased susceptibility to states of pleasure and pain are strictly unilateral. Associated with this overreaction to painful stimuli some loss of general sensation will always be manifest on the affected side of the body.

Pure cortical lesions cause no change in the threshold to pain, nor is there the exaggerated affective quality characteristic of thalamic lesions. Head and Holmes assume that both the thalamus and the cortex are concerned in conscious activity. They say:

"The most remarkable feature in that group of thalamic cases with which we have dealt in this work is not the loss of sensation, but an exces-

sive response to affective stimuli. This positive effect, an actual overloading of sensation with feeling tone, was present in all our 24 cases of this class." This effect is interpreted as due to the release of the inhibitory or regulatory influence of the cortex arising from the destruction of the ascending and descending fibers between the thalamus and the cortex, thus isolating the thalamus and allowing it to act to excess. These authors add, since "the affective states can be increased when the thalamus is freed from cortical control, we may conclude that the activity of the essential thalamic center is mainly occupied with the affective side of sensation." "This conclusion is strengthened by the fact that stationary cortical lesions, however extensive, which cause no convulsions or other signs of irritation and shock, produce no effect on sensibility to pain. Destruction of the cortex alone does not disturb the threshold for the painful or uncomfortable aspects of sensation."

Some recent experiments by Cannon have revealed a very intimate relation between emotion and some of the ductless glands. The suprarenal (or adrenal) glands, situated above the kidneys, secrete and pour into the blood a remarkable substance known as adrenalin or epinephrin. This substance exerts upon structures which are innervated by sympathetic nerves the same effects as are produced by impulses passing along those nerves. The glands may themselves be excited to activity by nervous impulses passing out through the sympathetic nerves. Cannon has shown that the emotions of fear, rage, and pain excite these glands to activity and cause the secretion of adrenalin. The blood of a caged cat which has been tormented by the barking of a dog will show an increased percentage of adrenalin. The addition of adrenalin to the blood has the further effect of causing liberation of sugar from the liver into the blood to such an extent that sugar may appear in the urine (glycosuria); and sugar is known to be the most available form in which energy can be quickly supplied to tissues which have been exhausted by exercise. Adrenalin will in this and other ways act as an antidote to muscular fatigue. It also renders more rapid the coagulation of the blood

If a muscle is fatigued, the threshold of irritability rises. It may rise as much as 600 per cent., but the average increase is approximately 200 per cent. If the fatigued muscle is allowed to rest, the former irritability is gradually regained, though two hours may pass before the recovery is complete. If a small dose of adrenalin is administered intravenously, or the adrenal

glands are stimulated to secrete, Cannon has found that the former irritability of the fatigued muscle may be recovered within three minutes. In this way adrenal secretion may largely restore efficiency after fatigue.

Fear and anger—as well as worry and distress—are attended by cessation of the contractions of the stomach and intestines. These mental states also reduce or temporarily abolish the secretion of gastric juice. Adrenalin injected into the body has the same effect. Besides checking the functions of the alimentary canal, adrenalin drives out the blood which, during digestive activity, floods the abdominal viscera. This blood flows all the more rapidly and abundantly through the heart, the lungs, the central nervous system, and the limbs.

Cannon epitomizes the account from which the above has been condensed in these words: "The emotional reactions above described may each be interpreted, therefore, as making the organism more efficient in the struggle which fear or rage or pain may involve. And that organism which, with the aid of adrenal secretion, best mobilizes its sugar, lessens its muscular fatigue, sends its blood to the vitally important organs, and provides against serious hemorrhage, will stand the best chance of surviving in the struggle for existence." It should be added that some of Cannon's observations have not been confirmed by more recent experiments of Stewart and others and some of his conclusions are controverted.

The preceding account includes a summary of some of the most securely established facts regarding the peripheral and central nervous mechanisms of painful impressions and the physiology of the emotions, together with a theoretical interpretation of the apparently twofold nature of pain as a specific sensation and as a component of the general affective state of the body as a whole. The more general questions concerning the physiological processes related with pleasurable and unpleasant experience and the affective life in general are still more difficult of analysis. It seems probable that pain, unpleasant and pleasurable feelings, emotion, and, in short, the entire affective life are very intimately related on the neurological side.

Many physiological theories of pleasure-pain have been elaborated, for

the most part on very slender observational grounds. It has been suggested that the flexor movements of the body are associated with pain, the extensor movements with pleasure; that constructive metabolism is pleasurable, destructive metabolism disagreeable; that heightened nervous discharge is pleasurable, and the reverse (some form of inhibition or of antagonistic contraction) is unpleasant. Some hold that pain and unpleasantness or disagreeableness are different in degree only, not in kind. Others regard pain as a true sensation, but disagreeableness and pleasure (affective experience) as belonging to a different category which is non-sensory. In the latter case the affective experience may be neurologically related in some way with the various sensations (including pain) or the affective experience and sensations may be independent variables with separate cerebral mechanisms. None of these hypotheses, or many others which might be mentioned, are competent to explain satisfactorily all of the known facts, though strong arguments can be adduced in support of each of them.

Our own view is that pleasurable and unpleasant experiences are not true sensations, that in the history of the psychogenesis of primitive animals a diffuse unlocalized affective experience of well-being or malaise probably antedated anything so clearly analyzed as a sensation with specific external reference, and that, parallel with the differentiation of true sensations of touch, temperature, and so on in consciousness, pain sensations emerged out of the diffuse affective experience and took their place among the other sense qualities. An essential condition for the appearance in consciousness of a definite sensation like touch or vision is the differentiation in the nervous system of a system of localized tracts and centers related to this function, and in the human body such localized tracts and centers seem to be present for pain. Pain, therefore, considered psychologically and neurologically, is a sensation, and a different neurological mechanism for unpleasantness and pleasantness must be sought. To this problem we shall next turn our attention.

We have seen above that it is possible to frame a neurological hypothesis which allows a given peripheral sensory neuron to be conceived as transmitting, say, a tactual impression from the skin and also a painful impression from the same or a different end-organ. Upon reaching the spinal cord the nervous impulses of the tactual series may pass through one type of spinal synapse to the spinal lemniscus, and finally reach the tactual center of the cerebral cortex, and the nervous impulses of the painful series may be drawn off through a second system of synapses for transmission through a distinct system of central pathways. Attention has also been called to the fact that the specific pain nerves and central paths may have been developed by a process of the further differentiation of separate neurons with different peripheral and central connections for these two functions. But what of the pleasurable qualities which seem similarly to be associated with some sensory impulses?

The simplest view seems to the writer to be that the normal activity of the body within physiological limits is intrinsically pleasurable, so far as it comes into consciousness at all. There is a simple joy of living for its own sake, and the more productive the life is, within well-defined physiological limits of fatigue, good health, and diversified types of reaction, the greater the happiness. The expenditure of energy within these physiological limits is pleasurable *per se* except in so far as various psychological factors enter to disturb the simple natural physiological expression of bodily

activity. Such disturbing factors are anxiety, want, rebellion against compulsory service, and unrelieved routine. The expenditure of intelligently directed nervous energy along lines of fruitful endeavor is probably the highest type of pleasure known to mankind.

A certain spontaneity of action, as Huxley long ago pointed out, is characteristic of all life and its natural expression gives rise to a primeval joy of living. Life in its fulness is more than immediate reaction to stimuli. As Max Eastman says in a delightful essay (The Will to Live, Jour. Philos., Psych., Sci. Methods, vol xiv, 1917, pp. 102–107), "We are not merely trying to adapt ourselves in order to stay alive, but we are trying also even more energetically to live. Everything we do and think is not a reaction; a great deal of it is action. . . . Life interflows with reality in full circles. We do things not only because we have a sensation, but also in order to make a sensation. And so do the most elementary organisms. Any rubber ball can react, but it requires life to act. And life does act. It seeks experience." This primitive reaching out of the organism for experience leads up to curiosity, the unquenchable impulse toward scientific discovery, and the divine fire of creative artistic genius. The evolutionary factor operating here is more than self-preservation; it is self-realization and fulfilment.

And it should be borne in mind that the normal activities of the body are all combined into adaptive systems, that is, they are directed toward the accomplishment of definite ends and not directed at random. Even in instinctive activities of the invariable or innate type, though there may be no consciousness of the end to be attained, the actions are not satisfying to the animal unless they follow in the predetermined adaptive sequence (p. 64). The play of both men and other animals is likewise always correlated around some definite physiological motive. And it is even more conspicuously true that the intelligently directed activities are unsatisfying unless they attain, or at least approximate to, some particular end. Stated in other words, it is not the activity which is pleasurable, so much as the accomplishment, or, in the case of delayed reactions, the hope of accomplishment.

The normal discharge, then, of definitely elaborated nervous circuits resulting in free unrestrained activity is pleasurable, in so far as the reaction comes into consciousness at all (of course, a large proportion of such reactions are strictly reflex and have no conscious significance). Conversely, the impediment to such discharge, no matter what the occasion, results in a stasis in the nerve centers, the summation of stimuli and the development of a situation of unrelieved nervous tension which is unpleasant until the tension is relieved by the appropriate adaptive reaction. Such a stasis may be brought about by a conflict of two sensory impulses for the same final common path (see p. 61), by the dilemma occasioned by the necessity for discrimination in an association center between two or more possible final paths, by fatigue, auto-intoxication, or other physiological states which lower the efficiency of the central mechanism, and by a variety of other causes. The unrelieved summation of stimuli in the nerve centers, involving stasis, tension, and interference with free discharge of nervous energy, gives a feeling of unpleasantness which in turn (in the higher types of conscious reaction at least) serves as a stimulus to other associated nerve centers to participate in the reaction until finally the appropriate avenue for an adaptive response is opened and the situation is relieved. With the release of the tension and

free discharge, the feeling tone changes to a distinctly pleasurable quality (see C. L. Herrick, 1910).

The fact that the primitive pain path in the spinal cord seems to follow a rather diffusely arranged system of fibers in the fasciculus proprius, frequently interrupted by synapses in the gray matter (Fig. 117) with correspondingly high resistance to nervous conduction, is perhaps correlated with this general and diffuse quality of unpleasantness.

Now, pain as a distinct and localizable sensation has not been involved in the situation described in the preceding paragraphs. Pain, considered as a distinct sensation, was, however, born out of this situation or differentiated from it. Certain sensational elements which have a high protective value for the organism are naturally most often involved in such a situation. These are warning calls, and usually necessitate an interruption of the ordinary business of life which may be in process at the time the danger threatens. The free flow of ordinary sensori-motor activity is abruptly checked, and the organism suddenly stops and makes the necessary readjustment as quickly as may be. In the interest of increasing the rapidity of this avoiding reaction, which, of course, is frequently of vital importance, the pathways of the exteroceptive pain reactions are well developed and segregated from the more diffuse and poorly organized affective apparatus which we have just been considering. Thus arose pain nerves (if such exist separately) and the pain tract of the spinal cord (whose anatomical distinctness seems well established), and also perhaps a special mechanism for painful reactions in the thalamus. Sherrington has given a graphic statement of the probable history of this process in the following words (Schäfer's Physiology, vol. ii, p. 974):

"The facility of path of these motor reflexes colligated to pain hints at their antiquity, or at their having been formed by some neural method particularly able to, as it were, make a good road. Each reaction that employs a neural path seems to smooth it by sheer act of travel. This is true even of slight impulses—light traffic—and more true of heavy. Pain reactions are to be regarded as very heavy traffic. Their impressions summate with peculiar ease, take correspondingly long periods to subside, and, to judge by their inertia, move generally masses of neural material relatively great. Such impressions might wear a road with quite especial speed. Many spinal reflexes imply, so to say, well-worn habits based on ancient pain reactions. One is almost emboldened to figuratively imagine them as connate memories of the spinal cord. The majority of them seem to be protective reactions that in organisms of high neural type are accompanied by 'pain.' "

But even in this case the apparatus for pain is incapable of acting as rapidly as are those of some other sensations. If a sensitive corn on the foot is struck a sharp blow, one will often feel a very distinct tactile sensation an appreciable interval before the painful quality is perceived, the latter, however, soon welling up into consciousness and obscuring the tactile quality entirely. This is an illustration of the fact that even the highly protective exteroceptive painful stimuli pass through a mechanism of slower reaction time than the primary exteroceptive sensations with which they may be associated.

We cannot here enter into a full discussion of the larger questions centering about the physiological correlates of the higher affective life, the emotions and esthetics. It has often been pointed out that the conscious processes resulting from exteroceptive stimulation tend to be directed

outward, the attention being focussed on the external objects giving rise to the stimuli with a minimum of personal reference. The deep sensations, both of the proprioceptive and the interoceptive group, on the other hand, have a less clearly defined local sign and the mental attitude toward them is not one of outwardly directed attention to the source of the stimulus, but rather a change in the subjective state and an alteration of the general feeling tone of the body as a whole. Under ordinary circumstances the visceral afferent and other deep nervous impulses do not come into clear consciousness separately, but in the aggregate these complexes (often termed as a whole common sensation) profoundly modify the general mental attitude and equilibrium. The generalized feelings of both the pleasurable and the painful type share this subjective reference with the common sensations. They are very important factors in that sensory continuum which lies at the basis of the maintenance of personal identity which the older psychologists sometimes called the empirical ego. Only the pains associated with the sharply localized cutaneous sensation qualities with a high adaptive value as warning signs of external danger have a distinct peripheral reference, and even this is less clearly defined than that of the accompanying sensations of pressure, and so forth. The deep pains are imperfectly localized and have more of the general subjective reference which has just been mentioned, and all of the pleasurable qualities are of this type.

The simpler affective types of experience, accordingly, seem to be most intimately associated with the "common sensation" complex, especially with the visceral sensation components of this complex. From this it has been argued that the coarser emotions, as well as the elementary feelings, are the direct expression in consciousness of these visceral activities, that the well-known visceral changes associated with the emotions are not the results, but the causes of the emotions (Lange and James). This hypothesis has been attacked experimentally by Sherrington (see The Integrative Action of the Nervous System, 1906, p. 260), who found that cutting the afferent sympathetic fibers from the abdominal viscera in dogs made no apparent difference in the emotional reactions of the animals; but the experiments are not very convincing, and the question is probably too complex for solution by so simple means as those here employed.

The probability is that we have here a circular type of reaction. The initial visceral afferent impulses, being heavily charged with affective qualities and with a minimum of objective reference, excite within the brain, probably in the medial thalamic nuclei, a general non-localized pleasurable or unpleasant feeling, a feeling of well-being or malaise, as the case may be. These thalamic receptive centers are in very intimate relation with the visceral efferent systems of the hypothalamus and a reflex response in the viscera follows—a typical organic circuit. So long as this circuit involves only the viscera and their thalamic centers the peripheral reference will be at a minimum, and the feeling remains an unlocalized change in the affective consciousness.

The higher emotional and esthetic activities are so charged with intellectual content also as to require the participation of the association centers of the cerebral cortex. But no pleasure-pain centers are known in the cortex and the evidence at present available seems to negative the presence of such centers. The agreeable or disagreeable components of the higher emotional processes are very probably due to the colligation of thalamic activities with cortical associational processes. In case these

emotional or esthetic processes are of cortical origin, that is, excited in the first instance by the activity of cortical associational centers, their affective content may be due to the involvement of the subcortical pleasure-pain apparatus in the associational process, and this apparatus would, as above described, generate efferent impulses from the related visceral centers, thus causing the characteristic visceral movements, which in turn would reinforce the visceral activities of the brain centers, and thus by a "back-stroke" action strengthen the emotional content of the primary associational complex. Thus the completion of the circular reaction may reinforce the affective consciousness so long as it is operative.

That pleasure is correlated with free discharge of nervous energy is suggested further by the fact that in most of the pleasurable emotions and sentiments there is present a large factor of recall of previous experiences. The esthetic enjoyment of a given situation is in large measure proportional to the wealth of associated memories incorporated within it, especially when these are recombined into new patterns. The pleasure experienced in listening to a complicated musical production like a symphony may be enhanced many fold after one has become thoroughly familiar with it, and still more so if the listener has himself played it or parts of it.

In concluding this discussion of pleasure-pain we quote the following paragraph from Sherrington's account of Cutaneous Sensations, already referred to (Schäfer's Physiology, 1900, vol. ii, p. 1000):

"Affective tone is an attribute of all sensation, and among the attribute tones of skin sensation is skin-pain. Affective tone inheres more intensely in senses which refer to the body than in those which refer to the environment, that is, it is strongest in the non-projicient senses. It is, therefore, strong in the cutaneous senses, and in them is inversely as their projicience, therefore least in touch spots, more in thermal spots, most in the so-called 'pain-spots.' . . . Stimuli evoking skin-pain are broadly such as injure or threaten injury to the skin; the skin may be said to have gone far toward developing a special sense of its own injuries. The central conducting path concerned with these skin feelings seems a side-path into which the impressions from the various skin spots embouch with various ease, those from the 'pain spots' especially easily. The physiological reactions connected with this side-path are characterized by tendency to 'summation,' tendency to 'collateral irradiation,' slow culmination, and slow subsidence. They often involve with their own activity that of adjacent sensory channels (associate pains, referred pains), and almost invariably of motor centers of visceral, facial, and other muscles of expression (emotional discharge)."

Our own view is in harmony with that expressed in this paragraph except that, while we recognize that sensations in general have an affective tone, we do not consider that affective experience is to be regarded as essentially an attribute or quale of sensation. These are independent variables which are, however, usually intimately associated. Each has its own mechanism. The mechanism of every sensation is a localizable system of tracts and centers as expounded in the preceding chapters. The mechanism of the affective experience is a more general neural attitude or physiological phase, intimately bound up with the visceral reactions peripherally and integrated centrally in the thalamus.

Summary.—In the human organism pain appears to be a true sensation with its own receptors, probably with independent

peripheral neurons (in some cases at least), and certainly with well localized conduction paths and cerebral centers, these centers being thalamic and not cortical. Pain appears to be closely related neurologically with feelings of unpleasantness and pleasantness, and these, in turn, with the higher emotions and the affective life in general. The intellectual elements in the higher emotions and sentiments are, of course, cortical. Nearly all cases of affective experience probably involve a highly complex interaction of cortical and subcortical activities. Pleasantness and unpleasantness are not regarded simply as attributes of specific sensory processes in any case, but rather as a mode of reaction or physiological attitude of the whole nervous system intimately bound up with certain visceral reactions of a protective sort whose central control is effected in the ventral and medial parts of the thalamus. These parts of the thalamus form, accordingly, the chief integrating center of the nervous reactions involved in purely affective experience. This mechanism is phylogenetically very old, and in lower vertebrates which lack the cerebral cortex it is adequate to direct avoiding reactions to noxious stimuli and seeking reactions to beneficial stimuli. With the appearance of the cortex in vertebrate evolution these thalamic centers became intimately connected with the association centers of the cerebral hemispheres, and an intelligent analysis of the feelings of unpleasantness and pleasantness became possible. As a final step in the development of the protective apparatus the peripheral nerves of painful sensibility, with their own specific conduction paths and centers, were differentiated, and pain takes its place among the other exteroceptive senses. But even in man the thalamic and visceral mechanisms of affective experience are preserved and give a characteristic organic background to the entire conscious life. In the normal man these mechanisms may function with a minimum of cortical control, giving the general feeling tone of well-being or malaise, or they may be tied up with the most complex cortical processes, thus entering into the fabric of the higher sentiments and affections and becoming important factors in shaping human conduct.

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CHAPTER XIX

THE STRUCTURE OF THE CEREBRAL CORTEX

THE preceding pages have included a brief chapter on some of the general biological principles underlying the differentiation of the structure and functions of the nervous system, some general characteristics of the nervous tissues, a brief survey of the structure of the various great divisions of the nervous system, and finally an analysis of the more important sensori-motor reflex circuits. Nearly all of the mechanisms hitherto considered are concerned with the innate invariable types of response represented in the reflex and instinctive life of the organism (p. 32). In the higher mammals, and especially in man, the individually acquired relatively variable types of action, particularly those which are consciously performed, require the coöperation of the cerebral cortex, and the following chapters will be devoted to a consideration of the cortex, its structure, functions, evolution, and biological significance.

We have already commented (p. 243) on the fact that the cerebral cortex appeared later in vertebrate evolution than most of the other parts of the brain, and that in general it serves the individually acquired and intelligent functions, in contrast with the brain stem and cerebellum, which contain the apparatus for the innate activities of the reflex type. The primary reflex centers of the brain stem and cerebellum, accordingly, are sometimes called the old brain (palæencephalon, see Fig. 45, p. 123), while the cerebral cortex and those parts of the brain stem which develop as subsidiary to the cortex (such as the neothalamus, p. 179) are called the new brain (neëncephalon).[1]

[1] A review of the evolution of the brain and the phylogenetic origin of the cerebral cortex would lie beyond the limits of this work, for the literature upon this subject is very extensive. The following papers may be

In the embryologic development of the human brain the cerebral hemispheres grow out as lateral pouches from the anterior end of the neural tube (Figs. 46–54, pp. 125–130). These pouches are hollow and the cavities within them are the lateral ventricles (also called the first and second ventricles), each of

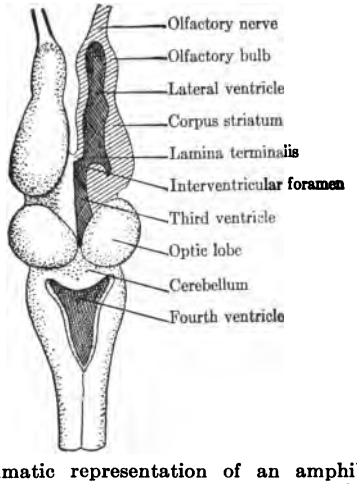

Fig. 119.—Diagrammatic representation of an amphibian brain from which the roof of the thalamus and cerebral hemisphere has been dissected off on the right side, exposing the third and the lateral ventricles and the interventricular foramen (foramen of Monro.) The membranous roof of the fourth ventricle has also been removed.

which communicates with the third ventricle of the thalamus by a narrow opening, the interventricular foramen or foramen of Monro.

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consulted in the present context. (See also the Bibliographies on pp. 174, 188, 250.)

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In a simply organized brain like that of the frog (Fig. 119) the olfactory bulb forms the anterior end of each cerebral hemisphere, behind which the massive wall contains ventrally the basal olfactory centers (p. 245), laterally the corpus striatum (p. 183), and dorsally the cerebral cortex or pallium (which has been removed on the right side of Fig. 119). In the human brain the cerebral cortex is so greatly enlarged that it overlaps all other structures of the hemisphere.

The anterior end of the early neural tube is an epithelial plate, the terminal plate or lamina terminalis, which forms the anterior wall of the third ventricle in the median plane. The position of this plate is unchanged throughout all subsequent stages of development (Figs. 46–51, pp. 124–128, and Fig. 119), though the cerebral hemispheres grow forward on each side of it, so that in the adult brain it lies deeply buried at the bottom of the great longitudinal fissure which separates the hemispheres.

The reflex centers of the two sides of the spinal cord and brain stem are connected by transverse bands of fibers known as *commissures*, for the facilitation of bilateral adjustments. There is an extensive series of ventral commissures crossing below the ventricle in the floor of the midbrain, medulla oblongata, and spinal cord, and several smaller dorsal commissures are found above the ventricle. In the diencephalon there is a large ventral commissure associated with the optic chiasma, and a dorsal commissure, the superior or habenular commissure, connecting the habenular bodies of the epithalamus. The basal parts of the cerebral hemispheres are connected by the anterior commissure, whose fibers cross in the lamina terminalis (Fig. 78, p. 180), and there are two large commissures which connect the cerebral cortex of the two hemispheres. One of these, the corpus callosum (Figs. 52, p. 128, and 78, p. 180), connects the non-olfactory cortex (neopallium, p. 243), the other one, the hippocampal commissure, connects the olfactory cortex (hippocampus). The fibers of the hippocampal commissure lie under the posterior end of the corpus callosum in close relation with the fimbria (Figs. 78, p. 180, and 80, p. 184).

In the smaller mammals the cerebral cortex is smooth, but in the larger forms it is more or less wrinkled, so that the surface

is marked by gyri or convolutions separated by sulci or fissures. A more highly convoluted cortical pattern is found in large animals than in smaller ones of closely related species, and in animals high in the zoölogical scale than in lower species; but the factors which have determined this pattern in each individual species are very complex (see Kappers, 1913 and 1914). The primary factor in the higher mammals has undoubtedly been the great increase in the superficial area of cortical gray matter without a corresponding enlargement of the skull.

The human cerebral cortex is somewhat arbitrarily divided into frontal, temporal, parietal, and occipital lobes (Fig. 120).

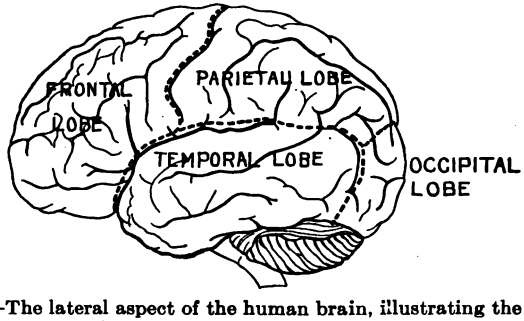

Fig. 120.—The lateral aspect of the human brain, illustrating the boundaries of the lobes of the cerebral cortex (cf. Fig. 54).

These lobes have no special functional significance, but are distinguished merely for convenience of topographic description. Some of the more important gyri and sulci are named on Figs. 52 and 54 (pp. 128 and 130). Between the temporal and frontal lobes and under the lower end of the lateral or Sylvian fissure is a buried convolution, the island of Reil (insula), which is seen in section in Figs. 79 and 80 (pp. 181 and 184). The cortical lobules which cover the insula are called opercula (Fig. 54, p. 130).

The walls of the cerebral hemispheres in the cortical region are very thick, the greater part of this thickness being occupied by white matter composed of nerve-fibers which effect various types of connection with the neurons of the cerebral cortex. The cortex itself is composed of gray matter and is relatively

thin, its inner border being marked by a broken line in Figs. 79 and 80. The subcortical white matter contains three chief classes of fibers: (1) Corona radiata fibers which connect the cortex with the brain stem (Figs. 79, 80). Most of these fibers pass through the internal capsule and comprise the sensory and motor projection fibers (pp. 180–186); (2) commissural fibers of the corpus callosum and hippocampal commissure (Figs. 79, 80); (3) association fibers, which connect different

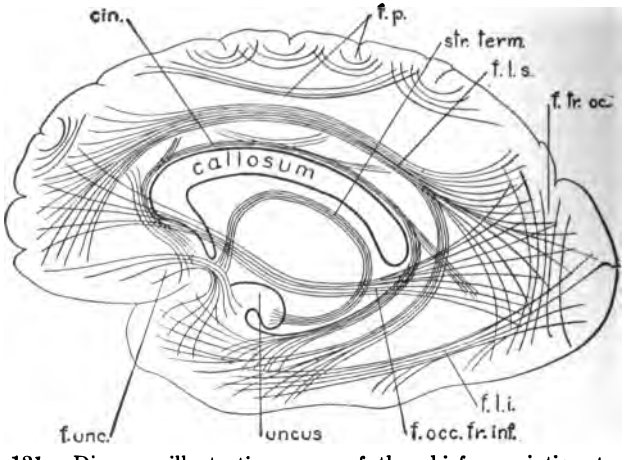

Fig. 121.—Diagram illustrating some of the chief association tracts of the cerebral hemisphere, seen as projected upon the median surface of the right hemisphere: *cin.*, cingulum; *f.l.i.*, fasciculus longitudinalis inferior; *f.l.s.*, fasciculus longitudinalis superior; *f.occ.fr.inf.*, fasciculus occipito-frontalis inferior; *f.p.*, arcuate fibers; *f.tr.oc.*, fasciculus transversus occipitalis; *f. unc.*, fasciculus uncinatus; *str. term.*, stria terminalis.

parts of the cerebral cortex of each hemisphere. Some of these fibers are very short, passing between adjacent gyri (arcuate fibers, or fibræ propriæ, *f.p.*, Fig. 121); others are very long fibers, forming compact fascicles which can easily be dissected out and which connect the important association centers of the cortex. All parts of the cerebral cortex are directly or indirectly connected with all other parts by these association fibers, so that no region can be regarded as the exclusive seat of any particular cortical function.

The human cortex varies in thickness in different regions

from about 4 mm. in the motor area to less than half that thickness in some other parts. When cut across and examined in the fresh condition it shows alternate bands of light and dark gray, whose arrangement varies in different parts of the hemisphere. The light bands are composed of myelinated

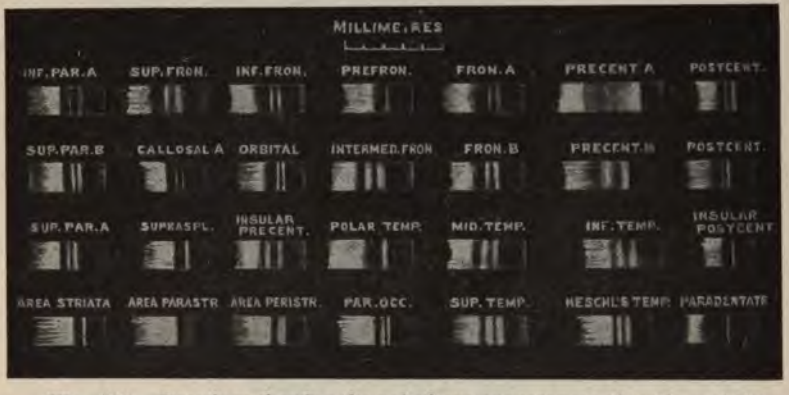

Fig. 122.—Drawings showing the naked-eye appearances of sections of the fresh cerebral cortex in different regions. (After Elliot Smith from Quain's Anatomy.)

The areas are named according to charts of the cortex published by Elliot Smith (1907; see also Quain's Anatomy, 11th ed., vol. iii, Part I, p. 373). The equivalent regions of Brodmann's charts (Figs. 130, 131, p. 307) are approximately as follows:

Area parastr. = area 18 in part; *Area peristr.* = areas 18, 19 in part; *Area striata* = area 17; *Callosal A* = areas 21, 23 in part; *Fron. B.* = lower parts of areas 8, 9, upper part of area 46; = *Henschl's temp.* = area 41 in part; *Inf. fron.* = areas 44 (anterior part), 45; *Inf. par. A* = area 39; *Inf. temp.* = area 20; *Intermed. fron.* = anterior border of lower lateral part of area 6; *Mid. temp.* = area 21; *Orbital* = *area* 47; *Paradentate* = area 36; *Par. occ.* = midlateral part of area 19; *Polar temp.* = area 38; *Postcent.* = areas 1, 2, 3; *Precent. A* = posterior part of area 4; *Precent. B* = anterior part of area 4; *Prefron.* = area 11; *Sup. fron.* = upper part of areas 6, 8, 9; *Sup. par. A* = area 7; *Sup. par. B* = area 5; *Supraspl.* (area parasplenialis) = areas 29, 30; *Sup. temp.* = areas 22, 41, 42.

fibers which run parallel with the surface. There are typically two of these light bands, in addition to the thin superficial white plexiform layer, the outer and inner stripes of Baillarger (Figs. 122 and 127). In the visual projection center (Figs. 130, 131, area 17) the outer stripe of Baillarger is greatly thickened by the optic projection fibers, and here it is some-

times called the line of Gennari. The portion of cortex exhibiting the line of Gennari is called the area striata (Figs. 130, 131, p. 307, area 17 and in modified form areas 18 and 19).

The most characteristic neurons of the cortex are pyramidal

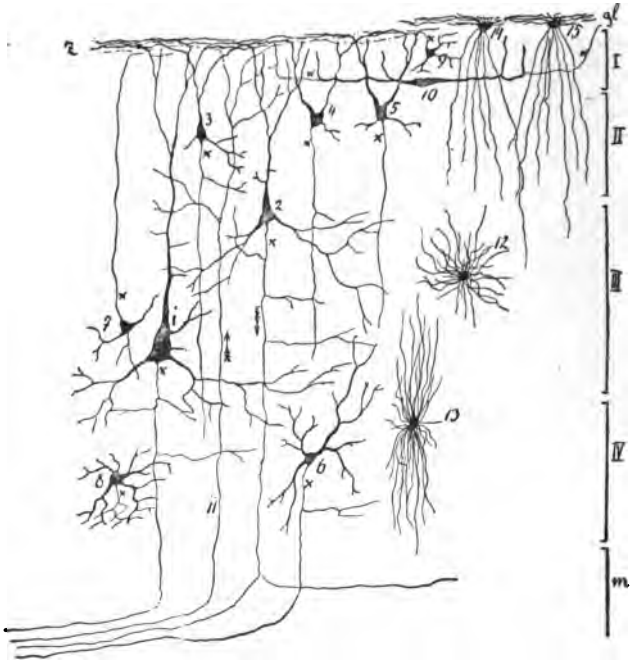

Fig. 123.—Diagrammatic illustration of the arrangement of neurons in the cerebral cortex as revealed by the Golgi method. The figure is copied from Obersteiner and the layers are numbered differently than in Brodmann's scheme, Fig. 127. Obersteiner's layer III includes layers III, IV, and V of Brodmann. The arrows indicate the direction of nervous conduction, and the axons of the neurons are marked by a cross, ×; *gl.*, layer of superficial neuroglia cells; *m*, beginning of the layer of white matter; 12, 13, 14, and 15 mark neuroglia (glia) cells; the other numbers designate different types of neurons.

in shape, with the apex directed toward the outer surface of the brain and prolonged to form the principal dendrite. Smaller dendrites arise from other parts of the cell body, and the axon arising from the base of the cell body is directed inward into the white matter (Figs. 7, 8, pp. 43, 45). The cortex contains,

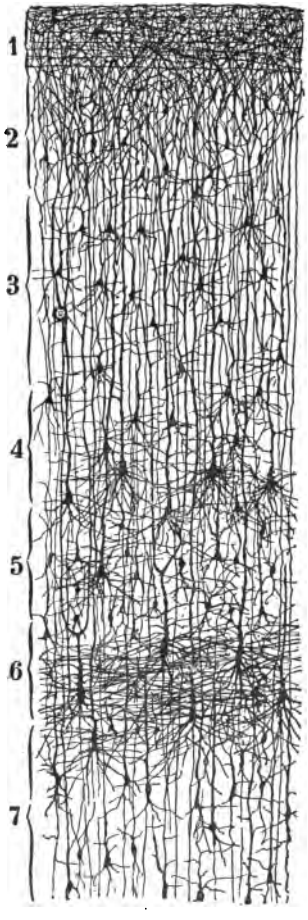

Fig. 124.—Section from the cerebral cortex of a human infant from the postcentral gyrus (gyrus centralis posterior), with the neurons impregnated by the method of Golgi. The figure is taken from Ramón y Cajal's Histology of the Central Nervous System, and the layers are numbered according to his system. Layer 1 corresponds to Brodmann's first layer (Fig. 127); layer 2, to his second layer; layers 3 and 4, to his third layer; layer 5, to his fourth layer; layer 6, to his fifth layer; and layer 7, to his sixth layer.

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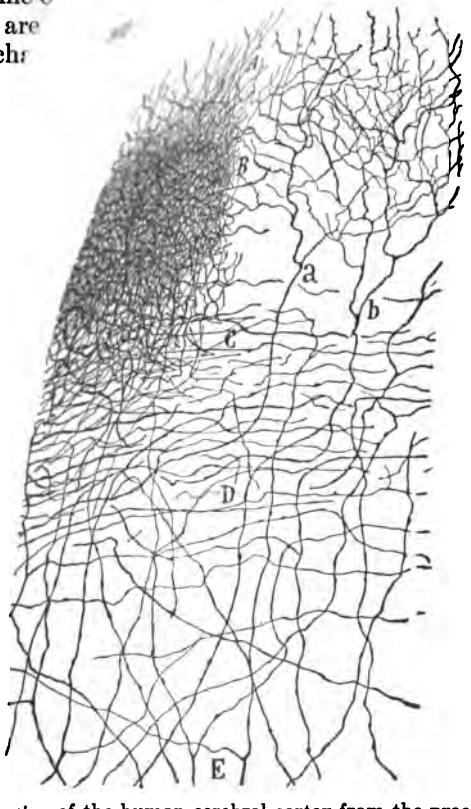

Fig. 125.—Section of the human cerebral cortex from the precentral gyrus (gyrus centralis anterior), illustrating the free endings of the incoming fibers. This region contains a large number of cells similar to those shown in Fig. 124; but none of the cells were stained in this preparation, which was prepared by the method of Golgi. At *a* and *b* are seen the terminal arborization of two individual fibers. At *B* is a dense entanglement of such terminal arborizations around the cell bodies of the pyramidal neurons of layer 3 (Fig. 124). *C*, *D*, and *E* illustrate horizontally directed nerve-fibers, from which the terminal arborizations shown in the upper part of the figure arise. (After Ramón y Cajal.)

Moreover, many other types of neurons, some of irregular shape (polymorphic or multiform cells) and many whose axons are short and ramify close to the cell body without leaving the cortex itself (Fig. 9, p. 45). These type II neurons probably assist in the summation and irradiation of stimuli (see p. 107). Some other types of neurons are shown in Fig. 123.

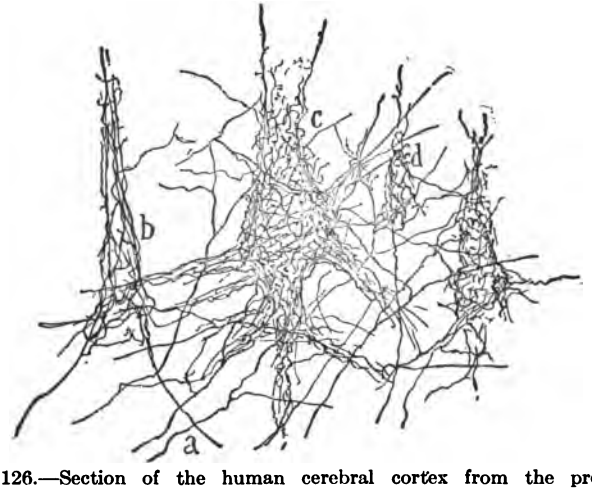

Fig. 126.—Section of the human cerebral cortex from the precentral gyrus, illustrating the details of the terminal arborizations of the incoming fibers (*a*) in the form of a closely woven feltwork of fibers (*b*, *c*, *d*) around the cell bodies of the large pyramidal cells of the cortex. The cells themselves are not stained in the preparation, but their outlines are clearly indicated by the pericellular basket-work by which they are enveloped. (After Ramón y Cajal.)

Figure 124 illustrates a typical arrangement of the neurons in the postcentral gyrus (g. centralis posterior of Fig. 54, p. 130). Most of the neurons here shown send their axons inward to participate in the formation of the white matter and may discharge their nervous impulses into remote parts of the brain. The endings of the afferent nerve-fibers which effect synaptic connection with the neurons here shown form a dense entanglement of fine unmyelinated fibers between the dendrites of these neurons. These afferent fibers are not included in Fig. 124;

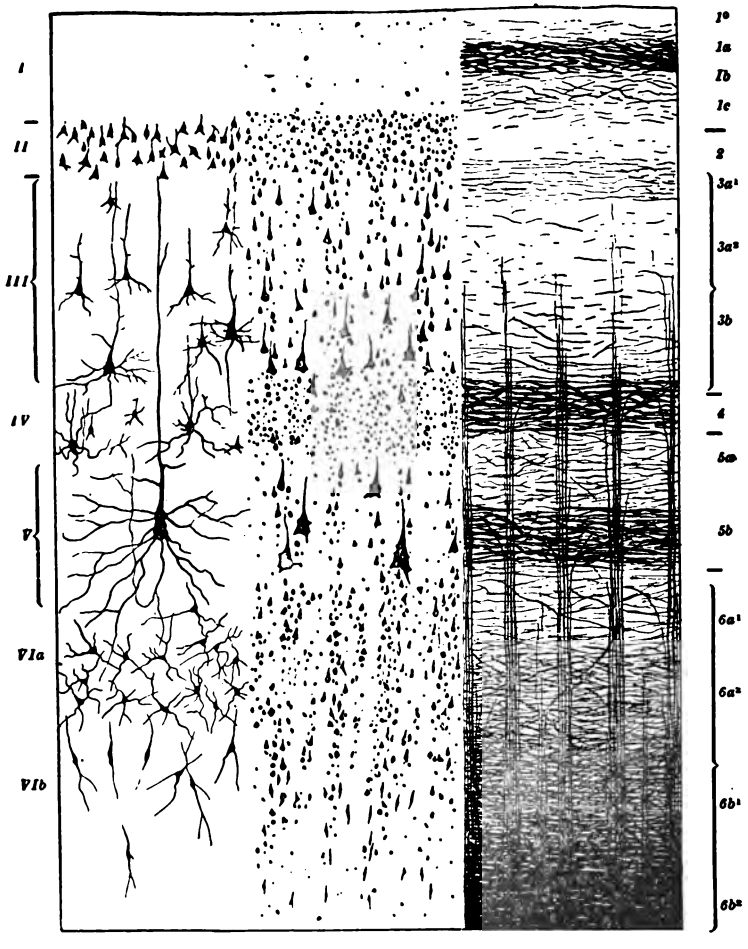

Fig. 127.—Diagram of the arrangement of the layers of cells and myelinated nerve-fibers in the cerebral cortex, according to Brodmann. At the left of the figure is shown the arrangement of cells as shown by the Golgi method, in the middle their arrangement as shown by Nissl's method, and at the right, the arrangement of nerve-fibers as shown by Weigert's method.

I. Lamina zonalis, or plexiform layer, containing tangential nerve-fibers.

II. Lamina granularis externa, or layer of small pyramidal cells.

III. Lamina pyramidalis, or layer of medium and large pyramidal cells.

one of them is shown in Fig. 123 and they are drawn separately in Fig. 125 as they appear in the precentral gyrus (gyrus centralis anterior of Fig. 54). These afferent fibers may be either sensory projection fibers or association fibers from other parts of the cortex. The synapses between these incoming fibers and the neurons of the cortex among which they end are of various types. Many of the afferent fibers end in the outermost layer of the cortex (layer 1 of Figs. 123 and 124) among the dendrites of the pyramidal cells which are here widely expanded (see Fig. 8, p. 45); others end in dense arborizations which closely envelop the bodies of the pyramidal cells (Fig. 126). Still others twine around the dendrites for their entire length. The dendrites of the pyramidal cells are very rough and thorny, and these thorns are supposed by some to be the points where the actual synaptic connections are effected.

Besides the lamination caused by the bands of tangential nerve-fibers already referred to, the cell bodies themselves are arranged in layers whose pattern varies in different parts of the cortex. Neurologists enumerate these layers differently. Brodmann, who has studied this question very exhaustively, enumerates six primary layers which in most parts of the cortex are arranged essentially as shown in the accompanying diagram (Fig. 127). The six layers here recognized are present in most but not in all parts of the cortex. In the different regions one or more of these layers may be reduced, enlarged, or subdivided; and on the basis of these differences the entire cortex has been mapped out into areas, each of which is defined by the arrangement of the layers of cortical cells and fibers.

Brodmann (Figs. 128, 129) divides the cerebral hemisphere into eleven general regions, which he says are recognizable more or less clearly throughout the entire group of mammals. These are:

IV. Lamina granularis interna, or inner granular layer, containing the medullated fibers of the external line of Baillarger (in the visual area called the stripe of Gennari).

V. Lamina ganglionaris, or layer of large cells, containing in the motor area the giant pyramidal cells or Betz cells, from which the fibers of the pyramidal tract arise, and containing in most areas the medullated fibers of the internal line of Baillarger.

VI. Lamina multiformis, or layer of polymorphic cells.

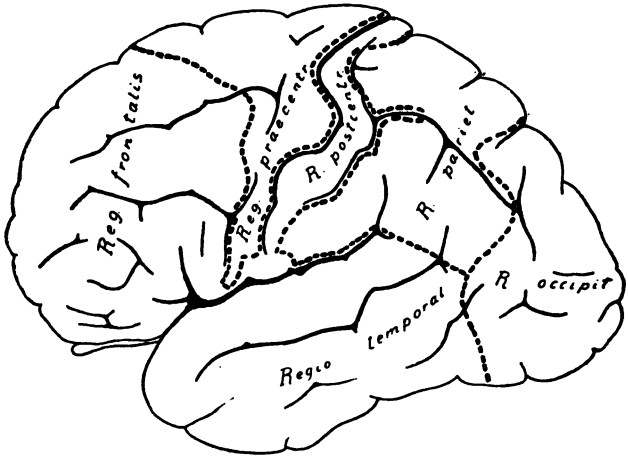

Fig. 128.—The chief regions of the human cerebral cortex as determined by Brodmann from the study of the structural arrangements of the layers of cells and fibers, seen from the left side.

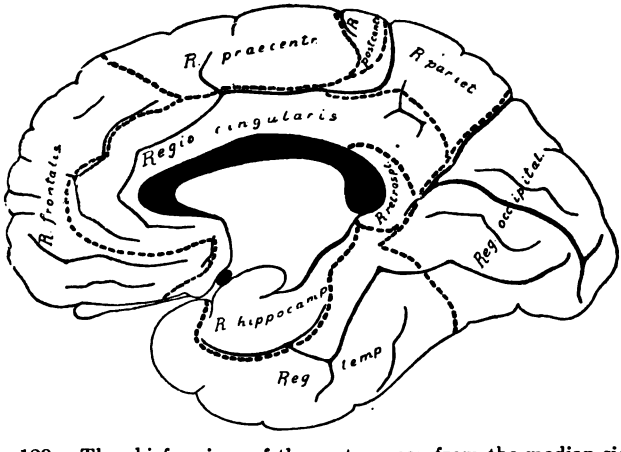

Fig. 129.—The chief regions of the cortex, seen from the median side.

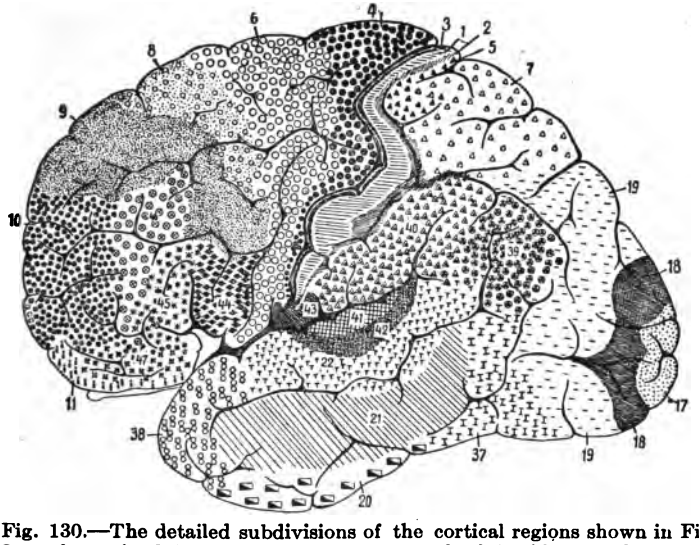

Fig. 130.—The detailed subdivisions of the cortical regions shown in Fig. 128 as determined by Brodmann, seen from the left side. Each area or field which is here designated by a number and conventional symbols has a distinctive lamination of its cells and fibers.

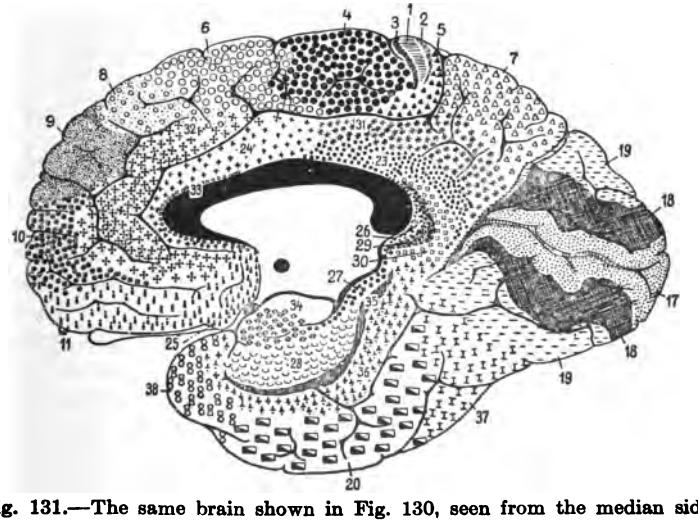

Fig. 131.—The same brain shown in Fig. 130, seen from the median side.

1. Regio postcentralis (tactile region).
2. Regio precentralis (motor region).
3. Regio frontalis (frontal association center).
4. Regio insularis (insula).
5. Regio parietalis (parietal association center).
6. Regio temporalis (auditory region).
7. Regio occipitalis (visual region).
8. Regio cingularis (supracallosal part of limbic lobe).
9. Regio retrosplenialis (postcallosal part of limbic lobe).
10. Regio hippocampica (gyrus hippocampi and hippocampus).
11. Regio olfactoria (uncus, amygdala, tuberculum olfactorium).

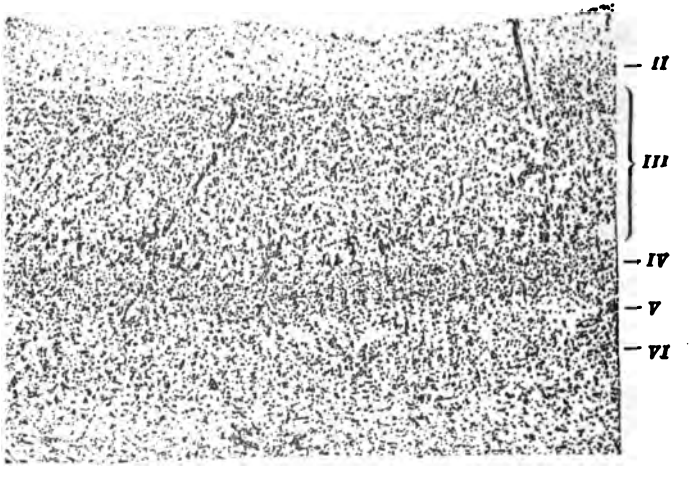

Fig. 132.—Arrangement of nerve cell bodies in the cortex of the postcentral gyrus (Field 3 of Brodmann, cf. Fig. 130). The cells are arranged in the six typical layers shown in Fig. 127. (After Brodmann.)

In the list as here given Brodmann's names of the regions are given, and in parenthesis is added a brief description of each region. Regions 8, 9, 10, and 11 are all concerned with the olfactory reactions, though region 8 only to a small extent. Region 11 is only in part cortical (the uncus); the other parts of this region are subcortical olfactory centers. The specific sensory and motor projection centers (see p. 180) lie within their respective regions, as designated, but they do not occupy the whole of their regions. On the basis of the arrangement of their cells and fibers these regions are further subdivided by

Brodmann into upward of 50 areas or fields, as shown in Figs. 130 and 131. The areas are less uniformly developed in different animals than are the general regions, though many of them are very constantly present. In the human brain the

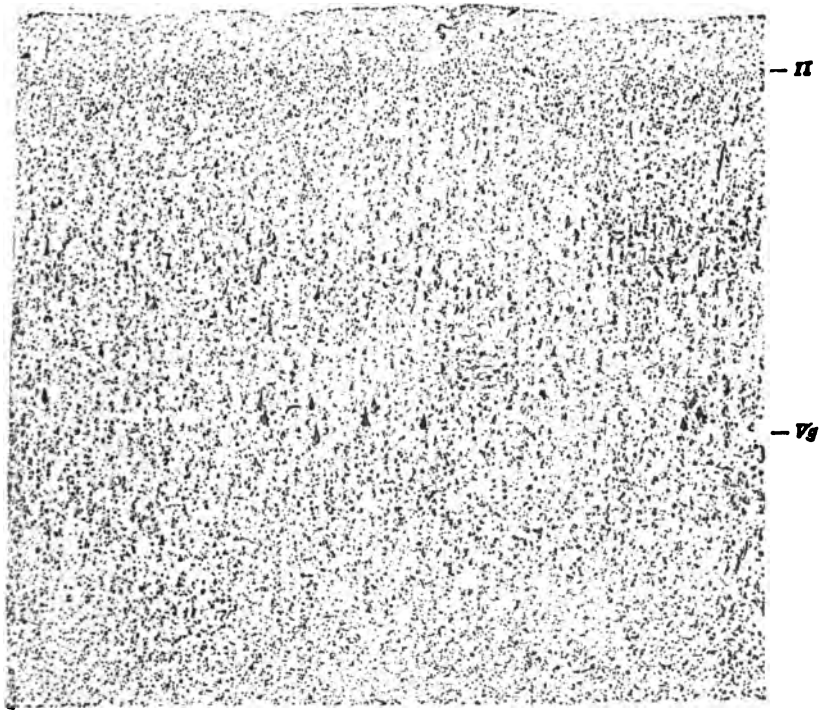

Fig. 133.—Arrangement of cells in the cortex of the precentral gyrus (Field 4, Fig. 130). This is the motor cortex; here the fourth, or internal granular, layer is absent. In the fifth layer are seen the giant pyramidal cells of Betz, from which the fibers of the pyramidal tract arise. (After Brodmann.)

arrangements of nerve cells in some of these areas are seen in Figs. 132, 133, and 134.

Bolton, Campbell, Ramón y Cajal, Vogt, Elliot Smith, and many others have investigated the lamination of the cerebral cortex in man and other mammals, and many charts similar to

those here presented have been published. The conclusions reached by these authors do not agree in all respects (particularly in the number of areas separately recognized and the nomenclature of the layers of cells and fibers in the various regions); nevertheless there is a sufficiently close general agreement to make it evident that there is a definite structural

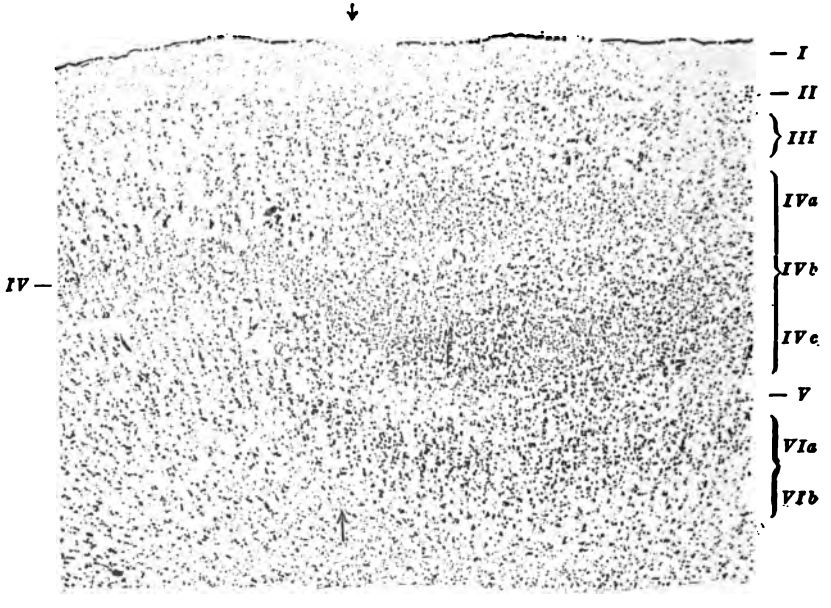

Fig. 134.—Arrangement of cells in the cortex of the visual area. The arrow marks the transition between the calcarine type of cortex on the right (Field 17, Fig. 131) and the adjacent occipital cortex on the left. The latter is (somewhat obscurely) six layered, but in the calcarine area the fourth, or internal granular layer is greatly thickened. (After Brodmann.)

pattern which is characteristic of the several cortical regions in each species of mammals, and that this pattern is broadly similar in all of the higher members of this group of animals.

Data derived from physiological experiments made on dogs, apes and other animals, and from the study of pathological human brains have shown also that the difference in structural pattern of the cortical areas is correlated with differences in

the functions performed by them. To these functional questions our attention will next be directed.

Summary.—The cerebral cortex is the organ of the highest individually modifiable functions, particularly those of the intellectual life. It matures late in both phylogenetic and individual development, and therefore has been called the neëncephalon. In early developmental stages it forms the roof of the lateral ventricle of each cerebral hemisphere, but in the adult human brain it is so enlarged as to envelop most other parts of the hemisphere. The cortex of the two hemispheres is connected by commissural fibers in the corpus callosum and the hippocampal commissure. The various regions of each hemisphere are connected by a complex web of association fibers, and some parts of the cortex are connected with subcortical regions by projection fibers. The sensory projection fibers discharge among the neurons of the sensory projection centers, and the motor projection fibers arise from neurons of the motor projection centers. The intervening association centers are connected with the projection centers and with each other by very intricate systems of association fibers. The cortex is laminated by bands of horizontally arranged nerve-fibers and by an arrangement of its cells in layers. The pattern of this lamination varies in different regions, and charts of these structurally defined regions are found to show a general correlation with the functionally defined areas as physiologically and pathologically determined.

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CHAPTER XX

THE FUNCTIONS OF THE CEREBRAL CORTEX

THE greatest diversity of view has prevailed and still prevails regarding the method of cortical function. That the cerebral cortex is concerned in some way with the higher conscious functions is clearly shown by a large body of experimental and clinical evidence.

The partial or complete removal of both cerebral hemispheres has been accomplished in various species of animals, from fishes to apes, and the changes in behavior carefully studied. In fishes and frogs the behavior is but little modified, save for the loss of the sense of smell, if the thalamus is left intact; but if the thalamus also is destroyed, the animal loses all power of spontaneous movement, of feeding when hungry, etc., though it will still react to some strong stimuli in an apparently normal manner. The fundamental reflexes of the spinal cord and brain stem are but little modified by this operation in frogs, save for the disturbance of the olfactory and visual functions. The recent experiments of Burnett have, moreover, shown that frogs in which the cerebral hemispheres alone have been removed are somewhat more excitable than normal frogs (probably due to the loss of cortical inhibitions), and that simple associations easily learned by normal frogs are in this case impossible. On the behavior of decerebrated birds see the papers by Rogers cited on page 188.

In the dog the loss of the cerebral hemispheres alone leaves the animal in a state of profound idiocy, though here also all of the primary sensori-motor reflexes (except the olfactory) remain if the thalamus is uninjured, and one such animal operated on by Goltz lived for eighteen months. During this time, however, he had to be artificially fed, for he had lost the ability to recognize food when set before him, nor did he show any of his former signs of intelligence. (These experiments are summarized in Schäfer's Physiology, vol. ii, pp.

698 ff., to which the reader is referred for references to the literature; see also the papers by Goltz, Edinger, and Holmes, cited in the appended Bibliography.)

More recently Karplus and Kreidl (1914) removed one or both cerebral hemispheres from a number of rhesus monkeys, none of which survived longer than twenty-six days after the operation. After complete removal of one hemisphere there were few enduring symptoms other than a defect of vision (hemianopsia) and muscular weakness and incoördination in the hand of the side opposite the injury. Upon removal of the remaining hemisphere from these animals, the hand partially paralyzed by the first operation was better controlled than the other hand; but movements of all kinds were poorly executed. Reflex responses followed cutaneous, optic and auditory stimulation. The monkeys were unable to feed themselves and in general were very helpless, apparently being reduced to a condition of profound idiocy. Cries made in response to painful stimuli were not accompanied by the normal mimetic movements.

Edinger and Fischer report the case of a boy who lived three years and nine months, whose brain when examined after death showed total lack of the cerebral cortex with no other important defects. In this boy there was practically no development in sensory or motor power or in intelligence from birth to the time of his death. The infant fed when put to the breast, but showed no signs of hunger, thirst, or any other sensory process. It lay in a profound stupor and during the first year of life made no spontaneous movements of the limbs. Until the time of death there was little change from this condition, save for continual crying from the second year on. This case shows that the reflex functions of the human brain stem are normally under cortical control to a much greater extent than are those of any of the lower animals, and that the absence of the cortex accordingly involves a more profound disturbance of the subcortical apparatus (see pp. 68, 145).

About a hundred years ago Gall and Spurzheim examined the brain, form of skull, and physiognomy of many persons whose mental characteristics were more or less fully known, and reached very definite conclusions regarding the localization

within the brain of particular mental faculties, such as benevolence, wit, and destructiveness; they claimed, further, that the sizes of these specific parts of the brain (and hence their relative physiological importance) can be determined by study of the external configuration of the skull. Many valuable observations were accumulated by these men and their followers, but the data were so uncritically used and the psychological basis of their generalizations was so faulty that the alleged science of phrenology which they founded is now wholly discredited and is professed today only by ignorant charlatans.

The great popularity of phrenology fifty years and more ago grew out of the fact that it served to give a pseudoscientific character to methods of reading character, and hence of forecasting the future formerly claimed by astrologers and necromancers. Modern psychology recognizes that the mind cannot be subdivided into any such distinct "faculties" as the phrenologists used, and modern neurology finds no basis for the sharply defined localization of these or any other mental functions, in the sense that a specific cortical area is the exclusive organ of a particular mental element.

As a reaction against the crude theories of Gall and Spurzheim it was commonly believed up to the year 1870 that there is no definite localization of functions in the cerebral cortex, but that the cortex functions as a whole, much like the cerebellar cortex, with no clearly defined functional areas. This view and modifications of it are still very prevalent. Goltz, who succeeded in removing all of both cerebral hemispheres from several dogs, holds that different psychic functions are not localizable in the cortex, but that removal of cortical areas simply diminishes general intelligence in proportion to the amount of cortex removed. Even total removal of the cortex, in his opinion, does not completely destroy consciousness. Many physiologists have, on the other hand, taught that particular conscious functions are localized in definite cortical areas, somewhat after the fashion of a refined and modernized phrenology, and this view is very prevalent among clinical neurologists.

The modern period of study of cortical functions was inaugurated by a chance observation on the battlefield. During the

Franco-Prussian war an army surgeon, Fritsch, while operating on a wounded soldier, applied the galvanic electric current to the exposed surface of the brain and observed a twitching of some of the muscles. This was followed immediately by experimental researches upon the electric excitability of the cerebral cortex of dogs, the first results of which were published by Fritsch and Hitzig in 1870. They showed that there are regions in the vicinity of the central sulcus (fissure of Rolando, cruciate sulcus) whose excitation in the living animal is followed by movements of definite groups of muscles on the opposite side of the body.

These observations have been followed by an immense number of experimental researches on various animals (the animals being anesthetized during the experiments) and clinico-pathological studies of the human brain, whose correlation and integration have proved very difficult. The most careful studies have, however, in general given concordant results. Without attempting a summary of these investigations here, we may mention the recent investigations of Sherrington on the chimpanzee, whose results as summarized on Fig. 135 may be accepted as fully in accord with the best previous experimental work, with the anatomical investigations of the regional differentiation of the cortex, and with the most recent clinical studies. The corresponding centers of the human brain are seen in Fig. 136.

The electric stimulation of each one of the shaded regions of Fig. 135 is followed by the contraction of a particular group of muscles on the opposite side of the body, as designated on the figure. The electrically excitable motor cortex is of two types, marked on the figure by stipple and vertical cross-hatching respectively. Stimulation of the latter areas in the frontal and occipital lobes calls forth conjugate movements of the eyes, and the physiological characteristics of these centers are very difierent from those of the centers in the precentral gyrus, which are shaded with stipple. This gyrus is the true motor projection center, and a comparison of Figs. 135 and 136 with Fig. 130 shows that its limits coincide tolerable closely with area 4 of Brodmann's chart of the ana-

tomically distinct cortical areas, including, however, a part of the cortex farther forward in area 6.

The structure of the cortex in the precentral motor area (Brodmann's area 4)is very characteristic. In this region the

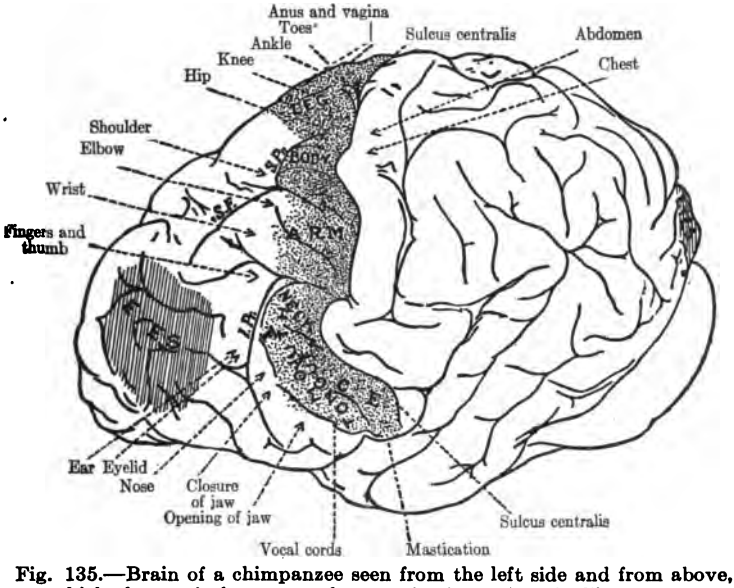

Fig. 135.—Brain of a chimpanzee seen from the left side and from above, upon which the cortical centers whose excitation causes bodily movements are indicated by shading. The regions shaded by vertical lines and marked "EYES" indicate the frontal and part of the occipital regions which when electrically excited cause conjugate movements of the eyes. The regions shaded with stipple comprise the motor projection centers from which the fibers of the pyramidal tract arise. The names printed large on the stippled surface indicate the main regions of the motor area; the names printed small outside the brain indicate broadly by their pointing lines the relative topography of some of the chief subdivisions of the main regions of the motor cortex. But there exists much overlapping of the motor centers and of their subdivisions which the diagram does not attempt to indicate. (After Grünbaum and Sherrington.)

fifth layer of the cortex (Figs. 127, 133) contains a type of large pyramidal cells (giant pyramids or Betz cells) which are found nowhere else in the brain. From these cells arise most of the fibers of the pyramidal tract (tractus cortico-spinalis). This connection has been proved in several ways in addition to the

direct physiological experiments by electric stimulation already referred to. First, if this area of the cortex (and a portion of area 6 in front of it) is destroyed, the entire pyramidal tract will degenerate, a result which follows from the destruction of no other part of the cortex. Conversely, if the pyramidal tract is interrupted, the giant pyramidal cells of this area are the only neurons of the cortex to give clear pictures of chromatolysis of their chromophilic substance. In the third place, these giant cells of the human cortex have been counted, and

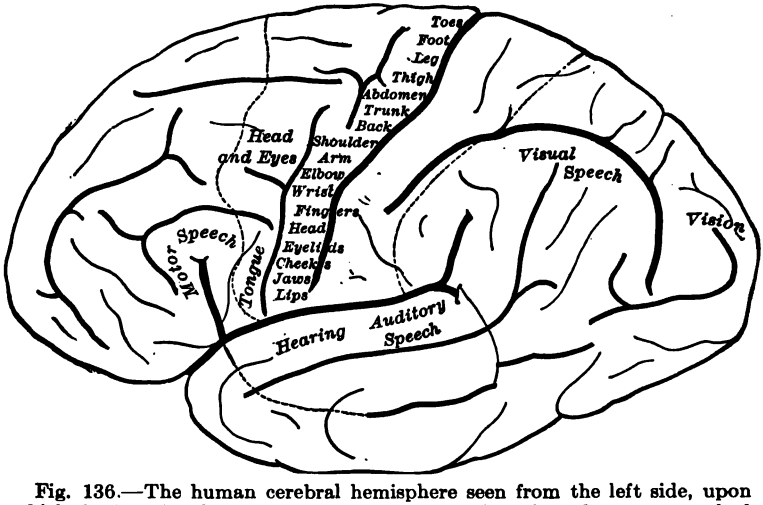

Fig. 136.—The human cerebral hemisphere seen from the left side, upon which the functional centers of the cortex are indicated. The center marked "motor speech" is Broca's convolution. (From Starr's Nervous Diseases.)

a count of the number of fibers in the pyramidal tract shows that the numbers are in tolerably close agreement (nearly 80,000 on each side of the body). Finally, a case of sclerotic degeneration involving almost the entire cortex has been described by Spielmeyer, in which these giant cells and the fibers of the pyramidal tract alone escaped injury.

Graham Brown and Sherrington in 1913 published some important observations on the functions of the motor cortex of the chimpanzee. After destruction of the motor cortex of the arm center in the left precentral gyrus there was temporary

loss of voluntary movement of the right arm, which was, however, soon restored and normal or nearly normal control of arm movements was finally regained. Some months later the arm center of the right precentral gyrus was destroyed. This was followed by temporary loss of voluntary movement of the left arm, with gradual return to nearly normal control. Subsequent destruction of the area of the right postcentral gyrus opposite the motor center of the arm resulted in some weakness and incoördination of movements of the left arm, which gradually improved. From their experiments they conclude that recovery of the use of an arm may take place fairly rapidly after the destruction of a large part—if not the whole—of the corresponding area of the motor cortex. This recovery is not due to regeneration of the area destroyed. It is not due to the taking over by the corresponding area of the opposite cerebral hemisphere of the movements of both arms. It is not due to the taking over by the postcentral cortex of functions of the motor cortex. The physiological processes involved in this recovery of cortical functions are as yet unknown (see fuller report by Leyton and Sherrington, 1917).

The pyramidal tract is one of the most important and best known conduction paths in the brain. This term is often applied to all motor projection fibers arising in the precentral motor centers; but recent usage inclines to limit its application to the spinal fibers only of this system (tractus cortico-spinalis), using the term tractus cortico-bulbaris for the fibers of this system connecting with the motor cranial nerves (p. 198).

The complete destruction of the pyramidal tract of one side, or of the motor cortex from which its fibers arise, causes partial hemiplegia, *i. e.*, loss of voluntary movement in the trunk and limbs of one side. If the associated cortico-bulbar fibers are likewise affected, the paralysis will affect the muscles of the head also on the same side as the limbs (total hemiplegia). If only a part of the fibers of the pyramidal tract are affected, a monoplegia will result, *i. e.*, loss of movement in only one limb or group of muscles.

These projection fibers and their cell bodies in the precentral cortex are known as the "upper motor neurons" and the clinical symptoms of motor defect resulting from their injury are in many respects different from those following destruction of the "lower motor neurons," *i. e.*, the peripheral neurons whose cell bodies lie in the ventral gray columns of the spinal cord. In the latter case the affected muscles will be flaccid and will rapidly waste away (flaccid paralysis). Their reflexes will be abolished and such patients show a complex of symptoms known as the reaction of degeneration. In upper motor neuron lesions the muscles retain their tone, which may be exaggerated (spastic paralysis); they do not waste away; and some of the reflexes will persist in a very characteristic form.

By these and other diagnostic signs it is usually possible for the neurologist to determine with considerable accuracy the site of an injury which destroys or impairs the voluntary motor path.

The exact mode of ending of the fibers of the pyramidal tract on their lower motor neurons has not been determined, and the relations here are very complex. It is probable that in most, if not in all cases a short neuron is intercalated between the upper and lower motor neurons in the spinal cord.

The sensory projection centers of the cortex have also been determined physiologically, though their limits are less precisely known than are those of the motor cortex. The olfactory receptive center has already been mentioned as comprised within the archipallium (hippocampus and hippocampal gyrus, see p. 243), only a part of which is exposed on the surface of the brain (the regio hippocampica of Fig. 129; areas 27, 28, 34, 35 of Fig. 131). The visual projection center, which receives fibers from the thalamic optic centers in the pulvinar and lateral geniculate body (pp. 180, 238), is in the occipital region (Fig. 129). Area 17 (Fig. 131) appears to be the chief center for the reception of these visual projection fibers, though the adjacent area 18 participates in this function, these areas together comprising the area striata of the cortex (p. 300). The auditory projection center is in the upper part of the temporal lobe (area 41, and probably to some extent area 42 also, of Fig. 130). The tactual projection center lies in the postcentral region (Fig. 128; areas 1, 2, and 3 of Fig. 130). The parts of the cerebral cortex which lie between the sensory and motor projection centers which have just been enumerated are the association centers (see pp. 326, 343).

Within each general sensory sphere there is a focal center which is exclusively receptive in function, such as area 17 (Fig. 131) in the visual sphere. Each of these focal centers is surrounded by others which receive projection fibers, though in less abundance, and also numerous association fibers from other parts of the cortex. These marginal fields are, therefore, to be regarded as association centers, each of which is under the dominant physiological influence of the adjacent focal projection center. These are sometimes called visual psychic, auditory psychic fields, etc., after the adjacent projection centers; but these terms are objectionable as implying the old

phrenological notion of localization of specific psychological faculties.

Each sensory projection center which receives afferent fibers of course sends out association fibers to other parts of the cortex. Some of these fibers may be very short, reaching only to the adjacent marginal fields (these are arcuate fibers, see Fig. 121, *f.p.*); other much longer association fibers may assist in forming the great associational tracts of the subcortical white matter. The association centers themselves are likewise connected by fiber tracts of bewildering complexity, so that every part of the cerebral cortex is in direct or indirect physiological connection with every other part. All of these parts are, therefore, able to influence the motor centers of the precentral gyrus, from which alone voluntary motor impulses can be discharged from the cortex to the lower motor centers of the brain stem and spinal cord.

The relations of the tactual and somesthetic sensory projection fibers to the postcentral and precentral gyri have been variously described, and some further consideration of the functional connections of these fibers may here be appropriate. From a large body of anatomical, experimental, and clinical evidence it was formerly assumed that the cortical motor centers are coextensive with those for the general somatic sensory projection systems of cutaneous and muscular sensibility, the projection centers of both the sensory and motor fibers related to each region of the body being located on both the anterior and posterior sides of the central sulcus or fissure of Rolando, that is, in both the precentral and postcentral gyri. Most of the diagrams of cortical localization in all but the most recent manuals are based upon this view of the case. But recent work has shown definitely that the motor centers are confined to the region in front of this sulcus. Here only are found the giant pyramidal cells of Betz which give rise to most of the fibers of the pyramidal tract. It may, therefore, be regarded as definitely established that motor projection fibers do not arise from the postcentral gyrus, as formerly supposed, though, as we have seen, the cortico-spinal and cortico-bulbar tracts are not the only pathways for efferent discharge from the cortex.

Sensory projection fibers, however, are known to pass from the general somatic sensory centers in the ventral and lateral nuclei of the thalamus to the postcentral gyrus, to the motor cortical centers of the precentral gyrus, and to other widely separated parts of the cortex. The significance of this fact is still obscure. That the postcentral gyrus is of different functional type from the precentral gyrus is shown by the fact that motor projection fibers arise from the latter and not from the former, by the differences in anatomical structure of these regions, by a large amount of experimental and clinical evidence which shows that tactile sensibility is not lost by the destruction of the precentral motor areas, and finally by direct physiological experiment upon human subjects.

Dr. Harvey Cushing (1909), in operating upon brain tumors in 2 cases

in which the use of an anesthetic was prohibited by the condition of the patient, exposed the postcentral gyrus and, with the patient's consent, electrically stimulated its surface. The patients, who were fully conscious during the operation, reported distinct cutaneous sensations which were subjectively localized as if coming from the skin of the hand. There were no motor responses from this and adjacent parts of the cortex behind the central sulcus, though in the same cases, upon stimulation of the precentral gyrus, motor responses were obtained which were accompanied by no sensations save those which came from the muscles during their contraction. In a previous similar case Dr. Cushing (1908) obtained typical motor responses from stimulation (with the patient's consent) of the precentral gyrus in an operation without anesthesia, and these responses were unaccompanied by painful sensations.

A very extensive series of experiments involving the stimulation and extirpation of these cortical areas in apes, dogs, and other animals supports the conclusion that the postcentral gyrus is the great receptive center for cutaneous reactions of the general cutaneous system. What may be the functions of those thalamic fibers which pass to the motor centers in front of the central fissure is unsettled. Possibly these connections are concerned in cortical reflexes of the proprioceptive system or acquired automatisms.

Direct evidence for this view is furnished by the case of surgical removal of the entire arm area of the precentral gyrus from a boy by Horsley (1909). The patient recovered and, after a period of temporary loss of both voluntary motion and sensation, regained partial voluntary control and a larger measure of sensibility. The most important residual sensory defect is astereognosis, or failure to recognize the forms of objects, and inaccuracy in localization of stimuli.

The myelinated fibers of the cerebral hemisphere mature, that is, acquire their myelin sheaths, at various stages in the development of the brain, some of these systems of fibers appearing before birth and some after birth. Much investigation has been directed to the determination of the exact facts regarding the sequence of development of these fibers, and many interesting theories have been developed regarding the significance of these facts.

Flechsig in a long series of researches made the first thorough study of this problem, and his conclusions have exerted a profound influence upon all subsequent theories of the functions of the cerebral cortex. He proposed a series of laws of developmental sequence (myelogeny) of the cortical fibers, among which two may be mentioned: (1) The myelinated fiber tracts of the brain do not all mature at the same time, and fiber systems which are of like function, that is, which are so connected as to perform special movements in response to excitation, tend to mature at the same time. This is Flechsig's "fundamental myelogenetic law," which may be stated in this form, The myelination of the nerve-fibers of the developing brain follows a definite sequence such that the fibers belonging to particular functional systems mature at the same time. (2) A second law states that in the cerebral cortex there are two great functional groups of

fibers which mature at different times. One of these groups contains the projection fibers, which mature early, chiefly before birth; the other group contains the association fibers, which mature after birth. These groups are further subdivided into subsidiary functional systems, each of which connects with a definite region of the cerebral cortex, so that it is possible to map the cortical areas in accordance with the sequence of development of the related myelinated fibers. There are, accordingly, two groups of cortical areas in this scheme: the projection centers whose fibers mature early and the association centers whose fibers mature late.

The arrangement of these areas as given in his latest publication (1920) is shown in Figs. 137 and 138. The numbers printed on the charts indicate the approximate order in which the corresponding parts acquire their myelinated fibers. Areas 1 to 10 are projection centers; areas 1 to 16 become myelinated before birth; 17 to 45, after birth. For a critical discussion of Flechsig's earlier work see Brodmann in Lewandowsky's Handbuch der Neurologie, Band I, pp. 234–244.

Attention should be called here to the fact that there are many different kinds of projection fibers, that is, fibers connecting the cerebral cortex with the underlying structures of the brain stem and spinal cord. Most of these projection fibers, except those of the olfactory system, pass through the corona radiata and internal capsule of the corpus striatum. The most important of these projection systems are the great sensory radiations which discharge their nervous impulses into the cortical centers of vision, hearing, touch, and smell, as already described (the exact course of the gustatory projection fibers has not been determined), and the great motor system of the pyramidal tract arising from the precentral gyrus. Each of the thalamo-cortical projection tracts of vision, hearing, and tactile sensibility is, moreover, accompanied by cortico-thalamic fibers which conduct in the reverse direction and whose functions are not well known, and there are other cortico-thalamic and cortico-mesencephalic systems. The cerebral cortex is in direct connection with the red nucleus of the cerebral peduncle by a cortico-rubral tract, arising in the frontal region of the cortex, and by ascending fibers from the red nucleus to the same general part of the cerebral hemisphere. From the frontal, parietal, temporal, and occipital association centers there arise large descending fiber tracts to the nuclei of the pons (cortico-pontile tracts). These connections between the cerebral cortex and the red nucleus and pons put the cerebral cortex and the cerebellum into very intimate relations,

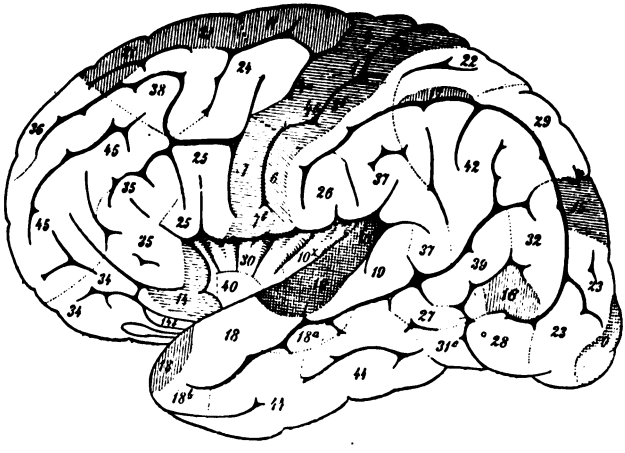

Fig. 137.

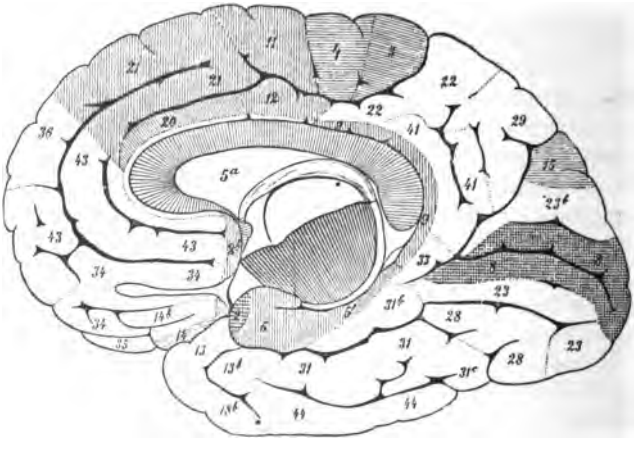

Fig. 138.

Figs. 137, 138.—Lateral and median views of the human cerebral hemisphere, to illustrate the sequence of maturity of the myelinated fibers of the cortex during the development of the brain, according to Flechsig's observations. The numbers indicate approximately the order in which different parts of the cortex acquire their mature fibers. (From Flechsig's Anatomie des Menschlichen Gehirns und Rückenmarks.)

but the exact way in which the cerebrum and the cerebellum coöperate functionally is obscure (see p. 216).

From the preceding account it is plain that the cerebral cortex is structurally differently organized in different parts, and that each of these parts has its own characteristic fiber connections. Physiological experiment and pathological studies have shown, moreover, that some of these regions, the projection centers, are functionally diverse, in that each one receives a particular type of afferent fibers or discharges efferent impulses into a definite subcortical motor center. Stated in other words, the cortex is structurally a mosaic of diverse patterns; and on the physiological side there is a specific localization of function, at least in the sense that the various systems of afferent and efferent projection fibers connect each with its particular place in the structural mosaic.

Several English neurologists, notably Bolton, from studies on the development and adult structure of the cortex in normal and abnormal men and in other mammals, have been led to the conclusion that, in addition to the mosaic localization pattern of which we have been speaking, there is a functional difference between the different layers of neurons of the cortex in general. Bolton believes that the granular layer (layer IV of Fig. 127) marks an important boundary between functionally different cortical mechanisms. The infragranular portion of the cortex is thought to be concerned especially with the performance of the simpler sensorimotor reactions, particularly those of the instinctive type, while the supragranular layers serve the higher associations manifested by the capacity to learn by individual experience and to develop the intellectual life.

The infragranular layers mature earlier in the development of the brain, and they are the last to suffer degeneration in the destruction of cortical cells in the acute dementias or insanities. The supragranular layers (notably the pyramidal neurons of Brodmann's third layer, Fig. 127) mature later than any other layers. They are thinner in lower animals and in feeble-minded and imbecile men than in the normal man, and they are the first to show degenerative changes in dementia.

This doctrine is controverted by some other neurologists, but the evidence seems to show that the supragranular pyramidal neurons are physiologically the most important elements in the higher associative processes of the cortex. In this connection it is significant that the granular and infragranular layers are thicker in the projection centers, while in the association centers the supragranular layers of pyramidal cells are thicker. But all of the layers in each region are very intimately related, the processes of most of the cells of the deeper layers extending throughout the thickness of the more superficial layers (see Figs. 123, 124, 125) to reach the most superficial layer, and in the present state of our knowledge a functional difference between the layers cannot be said to have been established, save in very general terms.

It must be borne in mind that the most significant parts of the human cerebral cortex are the association centers. These alone are greatly enlarged in the human brain as compared with those of the higher apes. In the latter animals the projection centers are fully as large as those of man, the much smaller brain weight being chiefly due to the relatively poor development of the association centers.

The data which we have summarized in the preceding pages have led to the most contradictory theories as to the exact mode of functioning of the association centers. Neurologists have been prone, even up to the present time, to fall into the error of attempting to find specific centers for particular mental functions or faculties. But the evidence at present available gives small promise of success in the search for such centers. It is, in fact, theoretically improbable that such discoveries will ever be made, for psychology today recognizes no such mosaic of discrete mental faculties as would be implied in such a doctrine.

The facts of cerebral localization as clinically and experimentally demonstrated, in themselves and aside from any philosophic theories based upon them, contribute no evidence whatever to a solution of the problem of a seat of consciousness or of particular mental "faculties." That the proper functioning of a given locus in the cortex is essential to the execution of a given motion or the experience of a given sensation by no means necessarily implies that the consciousness of the act is located there. The latter is an entirely independent problem which must be separately investigated. It is not, then, the facts of cerebral localization which can be called in question so much as the interpretation of these facts.

The search for a single seat of consciousness, such as psychologists and philosophers have so long sought, is vain. The higher mental processes undoubtedly require the activity of association centers of the cerebral cortex, and the integrity of the associational mechanism as a whole is essential for their full efficiency. The cerebral cortex differs from the reflex centers of the brain stem chiefly in that all of its parts are interconnected by inconceivably complex systems of associational connections, many of which are probably acquired late in life

under the influence of individual experience, and any combination of which may, under appropriate conditions of external excitation and internal physiological state, become involved in any cerebral process whatever.

Nevertheless, some of these cortical association paths are structurally more highly elaborated than others (Fig. 121, p. 298, illustrates the most distinct of these tracts), and certain combinations of cortical functions are, therefore, more likely to follow a given stimulus than others. This associational pattern is doubtless partly innate and partly acquired. That there is a fairly precise anatomical pattern of association tracts can be seen in any good dissection of the cerebral hemisphere, and that the elements of this pattern are related in definite functional systems which are spatially separate is shown by numberless clinical observations in which sharply circumscribed mental defects are found to be associated with definite cerebral lesions. The phenomena of aphasia give the clearest illustrations of these relations.

The term *aphasia* has commonly been applied to a variety of speech defects, but Hughlings Jackson extended the connotation of the word to include "a loss or defect in symbolizing relations of things in any way." The lesion which produces the defect affects the association centers rather than the projection centers, for there is no primary sensory defect—no blindness or deafness or loss of general sensation—nor is there any motor paralysis.

The problems connected with aphasia are very difficult and confused, and there is by no means general agreement on either the fundamental physiological mechanisms involved in speech or on the nature of the lesions which produce the various types of observed speech defects. The enormous literature relating to this subject cannot be summarized here; see the text-books of physiology, physiological psychology, and clinical neurology.

Lesions of the primary sensory or motor projection centers will not produce aphasia, for in these cases all sensations or all movements related to the injured parts are lost, whereas in aphasia only the correlations involved in speech or other associational processes are impaired and all other sensorimotor correlations may be intact. Of course, the number of associational pathways involved in the communicating of ideas by hearing, reading, speaking, and writing words is very large; and the character of

the speech defect will depend in part upon the particular associational tracts affected by the lesion and in part upon the effect of the lesion upon the general intelligence of the patient (diaschisis effect, see p. 329). The second factor seems to be exceedingly variable and has given rise to much controversy.

Distinctive names have been given to the more important types of speech defect as clinically observed; such as agraphia or inability to write correctly, aphemia or inability to utter words, word-blindness (alexia) or inability to comprehend written words, word-deafness or inability to comprehend spoken words, and many others. Evidently an aphasia may result from injury to (1) a sensory association area contiguous to the primary visual or auditory projection centers (sensory types of aphasia), or (2) to a motor association center contiguous to the motor projection centers for the speech muscles (motor types), or (3) to any of the associational tracts connecting these association centers.

The second, or motor, type of aphasia usually, though not invariably, results from injury to the posterior part of the inferior frontal gyrus (see Fig. 54, p. 130) of the left hemisphere in right-handed persons and of the right hemisphere in left-handed persons. This relation was first discovered by Broca, and the area of motor speech correlations (marked "motor speech" in Fig. 136, p. 318), has since been termed Broca's convolution.

It should be reiterated that Broca's convolution does not lie in the excitable motor zone of the cortex. Though the destruction of this area may be followed by defects of speech, the muscles of the larynx, tongue, lips, etc., involved in vocalization are not paralyzed. This case is typical of many other motor association centers of the cortex whose integrity is essential for specific motor combinations, though separate motor centers are present for all of the muscles involved in these movements.

The correlations involved in the motor functions of speech appear to be represented typically in only one hemisphere, though this is by no means rigidly true. The corresponding structures in the other hemisphere may coöperate in these functions normally, and after loss of speech from a unilateral lesion speech may be reacquired by further education of the uninjured centers of the same or the opposite side. It has recently been shown that Broca's convolution is often larger on the left side of the brain than on the right side and that the average thickness of the cortex in this region is greater on the left side.

Various attempts have been made to localize each of the various types of aphasia mentioned above in a specific part of the cortex, but with no concordant results. Each of these functions is, of course, very complex, and a small circumscribed cortical injury may disturb or temporarily abolish the entire complex by the destruction of one only of the component functional connections. (See the summary by Dr. A. Meyer, 1910.)

The problems of aphasia have recently been reviewed by Head (1920) on the basis of a study of a large number of military cases of local injury to one cerebral hemisphere. He concludes that "aphasia," "alexia," "agraphia," etc., as commonly defined, do not represent real clinical entities, but that each of these symptom complexes is produced by dissociation of some definite system of mental processes of the class which he terms "symbolic thinking and expression." What is lost in each case is a particular type of symbolism, and a number of these types of defect are analyzed and defined.

The general conclusion to be drawn from the entire series of physiological and pathological studies of the cortex is that specific mental entities are not resident in particular cortical areas, but that cortical functions involve the discharge of nervous energy from one or more sensory centers to various near and remote regions, each of which, in turn, may serve as a point of departure for new nervous discharges, and so on until the complexity of action and interaction of part upon part becomes too intricate for the mind to conceive. The resultant effect of all of these nervous activities which reverberate from one association center to another will be the establishment of some sort of a neural equilibrium which finds its expression in a definite motor act or an idea. The nature of this physiological process is still unknown.

This dynamic view of cortical function finds a further illustration in the realm of neuro-pathology in von Monakow's doctrine of *diaschisis*. The onset of cerebral hemorrhage or any other sudden injury to the cerebral cortex is usually marked by an apoplectic "stroke," with profound shock and usually loss of consciousness. The entire cortical equilibrium is disturbed and this effect irradiates very widely throughout the nervous system. If the injury is not too severe, there is soon a partial readjustment of the nervous equilibrium and consciousness returns. But the restoration is incomplete, for some of the normal factors in the dynamic equilibrium complex are lacking by reason of the destruction of the corresponding cortical areas or association tracts. The intelligence is enfeebled and all voluntary control is impaired. In the course of a few weeks or months a new equilibrium minus the lacking factors is established and the patient very rapidly improves. Ultimately complete recovery may occur, save for a permanent residual defect which results directly from the loss of the tissue destroyed.

The immediate shock-like interference with the activity of cerebral centers not directly affected by the lesion is what von Monakow means by diaschisis. Upon the restoration of the nervous equilibrium this transient diaschisis effect is wholly or partially lost, and the residual symptoms of defect give a fairly

accurate picture of the intrinsic functions of the center directly attacked by the lesion. It is commonly assumed that there is also during the process of gradual recovery from such a cortical injury a certain capacity for the compensatory development of other centers of the same or the opposite cerebral hemisphere, so that they learn to perform vicariously the functions of the lost part.

All functions of the nervous system are facilitated by repetition, and many such repetitions lead to an enduring change in the mode of response to stimulation which may be called physiological habit. This implies that the performance of every reaction leaves some sort of a residual change in the structure of the neuron systems involved. These acquired modifications of behavior are manifested in some degree by all organisms (see pp. 22, 33), and this capacity lies at the basis of all associative memory (whether consciously or unconsciously performed) and the capacity of learning by experience. This modifiability through individual experience is possessed by the cerebral cortex in higher degree than by any other part of the nervous system; and the capacity for reacting to stimuli in terms of past experience as well as of the present situation lies at the basis of that docility and intelligent adaptation of means to ends which are characteristic of the higher mammals. It is a fact of common observation that those animals which possess the capacity for intelligent adjustments of this sort have larger association centers in the cerebral cortex than do other species whose behavior is controlled by more simple reflex and instinctive factors, that is, by inherited as contrasted with individually acquired organization. This is brought out with especial distinctness by a comparison of the brains of the higher apes with that of man (Figs. 135, 136), and of the lower races of men as contrasted with the higher. In our own mental life we recognize the persistence of traces of previous experience subjectively as memory, and memory lies at the basis of all human culture. From this it follows that psychological memory is probably a function of the association centers; but it must not be assumed that specific memories reside in particular cortical areas, much less that they are preserved as

structural traces left in individual cortical cells, as has sometimes been done.[1]

The simplest concrete memory that can appear in consciousness is a very complex process, and probably involves the activity of an extensive system of association centers and tracts. That which persists in the cerebral cortex between the initial experience and the recollection of it is, therefore, in all probability a change in the interneuronic resistance such as to alter the physiological equilibrium of the component neurons of some particular associational system. What the nature of this change may be is unknown, but it is conceivable that it might take the form of a permanent modification of the synapses between the neurons which were functionally active during the initial experience such as to facilitate the active participation of the same neurons in the same physiological pattern during the reproduction.

That which we know subjectively as the association of ideas may, in a somewhat similar way, be pictured as involving neurologically the discharge of nervous energy in the cortex between two systems of neurons which have in some previous experience been physiologically united in some cortical reaction. If, for instance, I heard a song of a mocking bird for the first time last year while walking in a rose garden, upon revisiting the garden I may recall the song of the bird. Here the sight of the garden (a highly complex apperceptive process involving many association tracts) actuates neuron system number one dominated by present visual afferent impulses, and the association tract leading to neuron system number two (the auditory complex established last year when the song was heard) has a lowered physiological resistance by virtue of the previous collocation with system number one, and I remember the song (see p. 67).

It should be emphasized that the mechanism of association here suggested is purely theoretical; we have little scientific evi-

[1] These residua of past cerebral activities form the basis of those characteristic "brain dispositions" which are important factors in each personality. They have been termed "engrams" by Semon and "neurograms" by Morton Prince (see Prince, the Unconscious, Chapter V, New York, 1914); cf. the "physiological schema" of Head (Studies in Neurology, 1920, pp. 723ff.).

dence regarding the details of such physiological processes. But it can be confidently asserted that even the simplest associational processes are at least as complex as this, and may involve the participation of thousands of neurons in widely separate parts of the cortex; and the consciousness must be regarded as a function of the entire process, not of any detached center (cf. p. 69).

In summarizing this dynamic conception of the nature of consciousness I will quote a few sentences from my brother's writings (see C. L. Herrick, 1910, pp. 13, 14):

"The theory of consciousness which seems best to conform to the conditions of brain structure and its observed unity is that each conscious state is an expression of the total equilibrium of the conscious mechanism, and that intercurrent stimuli are continually shifting the equilibrium from one to another class of activities. In other words, the sensation accompanying a given color presentation is not due to the vibrations in the visual center in the occipital lobe, but to the state of cortical equilibrium or the equation of cortical excitement when that color stimulus predominates. Previous vestigial excitements and coördinations [associations, C. J. H., see p. 37] with the data from other cortical centers all enter into the conscious presentation. As the wave of excitation passes from the visual center to other parts, the proportional participation of other centers increases, producing a composite containing more distantly related elements."

"Every specific sense-content with its escort of reflexly produced associated elements causes a more or less profound disturbance of the psychical equilibrium, and the nature of this disturbance depends not only on the intensity and state of concentration, but very largely on the kind of equilibrium, already existing. . . . The character of the conscious act (and the elements of consciousness are always acts) will, of course, depend upon the extent to which the several factors in the associational system participate in the equilibrium. Each disturbance of the equilibrium spreads from the point of impact in such a way that progressively more of the possible reflex currents enter the complex, thus producing the extension from mere sensation to the higher processes of apperceptive association. A conscious act is always a fluctuation of equilibrium, so that all cognitive elements are awakened in response to changes rather than invariable or monotonous stimuli."

In connection with physiological studies on the facilitation of function of a given cortical area by stimulation of other functionally related areas Graham Brown (1916) presents some facts which support such a conception of cortical function as a fluctuating dynamic equilibrium of the whole apparatus, together with very interesting suggestions regarding the probable types of cortical activity in association, fatigue, attention, interest, and the like.

The dynamic view of consciousness here adopted makes such expressions as "the unconscious mind" impossible contradictions. Either the mental functions are in process or they are

not, and unconscious cerebration is not consciousness. This is, of course, not incompatible with a dissociation of consciousness into multiple or co-conscious units, as Dr. Morton Prince so forcibly illustrates (The Unconscious, p. 251), though how far in normal men this dissociation may be carried is an open question.

In my life as viewed by an outside observer there is continuity of process, but not necessarily continuity of consciousness. In my own experience consciousness appears to be continuous, of course, because the periods of unconsciousness (as in coma, deep sleep, etc.) do not appear in consciousness; that is, they do not exist for me except as I learn of them by an indirection. In a water mill the function of grinding corn may go on intermittently, though the mechanism is there all the time and the energy is there; but if the water passes from the mill race out over the dam instead of through the water wheel the grinding function ceases. While the mill is at rest changes may be made in the machinery which will modify the character of the grinding when it is resumed, but these changes are not grinding. So in the brain the mechanism of consciousness and the structural memory vestiges of past experience may be present continuously; indeed, these vestigeal traces may be linked up in new ways by intercurrent physiological processes. But these things do not constitute consciousness. In fact, a large amount of unconscious cerebration may go on, the end result of which alone becomes conscious. The aim of physiological psychology is to clarify not only the mechanism of consciousness, but also all of the antecedent and subsequent physiological processes which are, from the standpoint of an outside observer, demonstrably related to the conscious processes. It is possible, moreover, to develop a really scientific introspective psychology in which abstraction is made from all of these mechanisms and the individual experiences alone are studied as given in consciousness. This makes up a large part of general psychology.

Summary.—The functions of the cerebral cortex are still largely wrapped in mystery, but the evidence thus far accumulated suggests that these functions are, so far as physiologically known, not different in kind from those of the other parts of the

brain. It is, however, manifest that these functions are concerned with the individually acquired and especially the intelligently performed activities as distinguished from the fundamental reflex and instinctive processes whose mechanisms are innate. There is a specific localization of function in the cerebral cortex, in the sense that particular systems of sensory projection fibers terminate in special regions (the sensory projection centers), that from other special regions (the motor projection centers) particular systems of efferent fibers arise for connection with the lower motor centers related to groups of muscles concerned with the bodily movements, and that between these projection centers there are association centers, each of which has fibrous connections of a more or less definite pattern with all other parts of the cortex. The destruction of any part of the cortex or of the fiber tracts connected therewith involves, first, a permanent loss of the particular functions served by the neurons affected, and, in the second place, a transitory disturbance of the cortical equilibrium as a whole (diaschisis effect). Specific mental acts or faculties are not resident in particular cortical areas, but all conscious processes probably require the discharge of nervous energy throughout extensive regions of the cortex, and the character of the consciousness will depend in each case upon the dynamic pattern of this discharge and the sequence of function of its component systems. This pattern is inconceivably complex and only the grosser features are at present open to observation by experiment and pathological studies.

No cortical area can properly be described as the exclusive center of a particular function. Such "centers" are merely nodal points in an exceedingly complex system of neurons which must act as a whole in order to perform any function whatsoever. Their relation to cerebral functions is analogous to that of the railway stations of a big city to traffic, each drawing from the whole city its appropriate share of passengers and freight; and their great clinical value grows out of just this segregation of fibers of like functional systems in a narrow space, and not to any mysterious power of generating psychic or any other special forces of their own.

The essence of cortical function is correlation, and a cortical

center for the performance of a particular function is a physiological absurdity, save in the restricted sense described above, as a nodal point in a very complex system of associated conduction paths. Those reflexes whose simple functions can be localized in a single center have their mechanisms abundantly provided for in the brain stem. The cerebral cortex of the resting brain is probably in a state of incessant activity, *i. e.*, it possesses a certain physiological "tone." This activity may be conceived as a system of equilibrated nervous discharges. This is not necessarily a conscious process, but it has a characteristic pattern in each individual which lies at the basis of his disposition or mental type. An effective stimulus disturbs this equilibrium and the precise effect will depend upon variable synaptic resistance or neuron thresholds which change with different functional states of the organism as a whole and of the brain in particular. If this activity involves the cerebral cortex of a human brain, it may be a conscious activity, the kind of consciousness depending on the kind of discharge. But the consciousness must not be thought of as localized in any cortical area. The discharge in question may reverberate to the extreme limits of the nervous system and the peripheral activities may be as essential in determining the conscious content as the cortical.

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CHAPTER XXI

THE EVOLUTION AND SIGNIFICANCE OF THE CEREBRAL CORTEX

At the conclusion of our analysis of the structure and functions of the nervous system it will be of interest to review very briefly a few topics of a more general sort related to our theme, with special reference to the significance of the cerebral cortex in the general scheme of human evolution and culture.

For the purpose of our analysis animal activities may be classified under three heads (see p. 32): (1) Innate functions of invariable or stereotyped character developed through natural selection or other biological processes, whose mechanism is hereditary and common (with small differences only) to all members of a race or species, typified by reflex action and purely instinctive action; (2) variable and modifiable functions, whose pattern is determined by individual experience through which the innate action system is more or less permanently altered, intelligent acts and the reasoning process representing the highest forms of this type, though the lower members of this series are not necessarily consciously performed; (3) acquired automatisms, or individually acquired actions which have become so thoroughly habitual as to be performed quite as mechanically as the hereditary reflexes. Intelligently acquired actions which have finally come to be automatically and even unconsciously performed are sometimes designated "lapsed intelligence," but such lapsed intelligence must be a purely individual acquisition. There is no evidence that automatisms of this sort can be transmitted in heredity, and, therefore, they can play no part directly in the evolution of instincts, as some have taught.

The first and second of the types of action above distinguished appear to be common to all organisms, though their relative importance varies enormously from species to species. The

first type includes the reflexes and all of the pure instinct-actions, that is, the hereditary component of the commonly recognized instincts (p. 64). There is no clear boundary between reflexes and instinct-actions as just defined. These actions may be exceedingly complex and their neuro-muscular mechanisms may be complicated apparently without limit. The available evidence suggests that they are always unconsciously performed.

Most of our common activities include all three of these types of behavior in varying proportions, and accordingly they frequently have not been distinguished. The first and third types are especially liable to confusion, for both are manifested as stereotyped, non-intelligent behavior. They can sometimes be separated only by a study of their origins; nevertheless this distinction is of great importance, especially to educators.

The nervous organs of the invariable reactions are fairly well known and are characterized in their more highly elaborated forms by a closely knit system of nerve-centers and distinct connecting fiber tracts so organized that particular stimuli may call forth a response or a combination of several responses selected from a fixed number of possible actions. The range of possible reactions of any given functional system of this type is limited by the structural complexity of the nerve-centers involved. This complexity may be very great, with a correspondingly great number of movements necessary to complete the reaction, and it may include the capacity for discriminating between two or more structurally possible modes of response by means of variable internal functional states of the nerve-centers. But in all of these cases the response is finally determined within rather narrow limits by the nature of the stimuli and the innate structural organization not only of the nervous organs, but of the body as a whole.

In some cases an elaborate nervous reflex or instinctive act may involve a more extensive nervous apparatus than is required by an intelligent act. It is not a mere question of the size of the nervous mechanisms involved. For instance, a comparison of the brains of the two species of fishes shown in

Fig. 139 shows that in the medulla oblongata of these rather closely related species there is an astonishing difference between the size of certain reflex centers. The greater size of the medulla oblongata of Carpiodes over that of Hyodon is due almost entirely to the enlargement of the centers for taste,[1] and these reflex centers are found to be very complex. The enormous increase in the mass and complexity of arrangement of

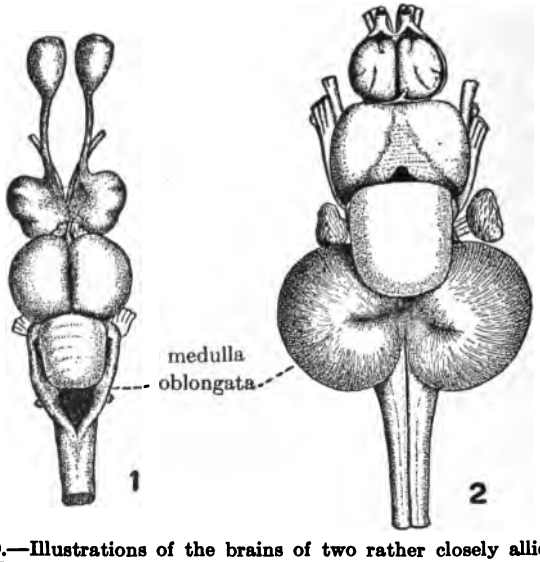

Fig. 139.—Illustrations of the brains of two rather closely allied species of fishes showing very different development of the reflex centers of the medulla oblongata: (1) Hyodon tergisus, the moon-eye, (2) Carpiodes tumidus, a carp-like species. (After C. L. Herrick.)

the gustatory neurons in Carpiodes does not imply any higher organization from the standpoint of range of behavior (see p. 19) than in Hyodon. The apparatus is more efficient as a means of sorting out food particles from mud, but we do not rank this form of activity very high in our scale of behavior.

In general, in the execution of a complicated reflex many

[1] For an analysis of this gustatory apparatus in fishes, see HERRICK, C. JUDSON. The Central Gustatory Paths in the Brains of Bony Fishes, Jour. Comp. Neurol., vol. xv, 1905, pp. 375–456.

interconnected nerve-centers are so arranged that they discharge into a common final path or an integrated series of such coördinated paths. The movements involved in the act, if performed at all, must follow in a definite sequence which is structurally predetermined in the inborn organization of the nerve-centers concerned. In the variable type of response, on the other hand, the association centers involved are so arranged that many final paths leading to different systems of coördinated motor centers diverge from a single center of correlation. Which of these paths will be taken in a given reaction, that is, which of several possible different (or even antagonistic) movements will result, will be determined by variable physiological factors of internal resistance within the correlating system (fatigue, habit, the influence of memory vestiges, etc.); accordingly, the response is not predetermined by the inborn organization of the apparatus.

Definite, well-established reflexes generally follow distinct nervous pathways between sharply limited nerve-centers. Between these centers there is usually found, in addition to the well insulated tracts just mentioned, a more diffuse and loosely organized entanglement of nerve-cells and fibers, through which nervous impulses may be more slowly transmitted in any direction. Tissue of this character is found throughout the entire length of the central nervous system, and in some places it occupies extensive regions (especially in the medulla oblongata and upper part of the spinal cord) which are termed the reticular formation (see pp. 69, 137, 172).

The reticular formation is the parent tissue out of which the higher correlation centers have been differentiated. In the spinal cord and medulla oblongata, where its character is most clearly seen, it receives fibers from all of the sensory centers and may discharge motor impulses into efferent centers of contiguous or very remote regions. In the higher parts of the brain the elaborate association centers of the thalamus and cerebral hemispheres have been developed from such a primitive matrix, and these centers are interconnected by similar undifferentiated nervous tissue.

The details of the functional connections of the reflex centers of the brain stem are much more precisely known than are

those of the higher correlation centers of the thalamus and cerebral cortex. And, in fact, it is essential that these details be fairly well understood before the functions of the higher centers can be investigated; for all nervous impulses which reach these higher centers must first pass through the lower centers and there be combined into reflex systems or otherwise correlated. The afferent stimuli which reach the cerebral cortex are not crude sensory impressions, but purposeful reflex combinations, often including sensory data from several different sense organs.

The nerve-centers of the spinal cord and brain stem in general are of this more rigid type, the internal adjustments of the system being, for the most part, as mechanically determined as are those of an automatic telephone exchange. The cerebellum is the highest member of this series, exerting a regulatory and reinforcing influence upon all of the other members. Nevertheless the cerebellum adds no new types of reaction or combinations of reactions to those of the brain stem; its cortex shows little demonstrable localization of different functions, and its efferent tracts are physiologically related to a limited number of pre-established systems of motor coördination in the brain stem and spinal cord. In all of these respects the contrast between the cerebellar cortex and the cerebral cortex is very striking.

The variable or individually modifiable type of reaction is served chiefly by the cerebral cortex and its immediate dependencies, though some capacity of this sort is found in the brain stem, as shown by the behavior of lower vertebrates which lack the cerebral cortex. This type of reaction is genetically related with that modifiability arising from variable internal physiological states which we have mentioned as present in the reflex centers. There is no proof that the simpler forms of this individually modifiable behavior are conscious, though the higher forms are certainly so.

The cerebral cortex can in no case act independently of the reflex centers of the brain stem, but always through the agency of these centers. It is superposed upon them much as the cerebellum is, though the control exerted is of a very different type. Here there is a very elaborate regional differentiation of the

cortex with an infinite complexity of associational connections. The efferent pathways, moreover, are not physiologically homogeneous; but they are so diversified that any possible combination of the organs of response may be effected by associations within the cortex. The various afferent functional systems enter sharply circumscribed cortical areas (the sensory projection centers); and the efferent fibers likewise leave the cortex from functionally defined motor areas, each group of muscles which coöperate in definite reaction complexes (termed synergic muscles, see p. 36) being excited from a definite part of the motor cortical field, whose motor tract is anatomically distinct throughout its entire further course from the cortex to the periphery. Between the sensory projection centers and the motor areas are interpolated the association centers, and these are so arranged that all correlation, integration, and assimilation of present sensory impulses with memory vestiges of past reactions are completed, and the nature of the response to be made is determined before the resultant nervous impulses are discharged into the motor centers. Only such of the motor areas will be excited to function as are necessary for evoking the particular reaction which is the appropriate (that is, adaptive) response to the total situation in which the body finds itself. This arrangement of association centers in relation to a series of distinct motor areas provides the flexibility necessary for complex delayed reactions whose character is not predetermined by the nature of the congenital pattern of the nervous connections.[1]

The thalamus, as we have seen (p. 179), has its own intrinsic system of association centers which discharge downward into the cerebral peduncles, and this is the primary reflex apparatus of this part of the brain. The thalamo-cortical connections arose to prominence later in the evolutionary history, though feeble rudiments of these are present in lower brains. Parallel with the enlargement of these cortical connections a special part of the thalamus was set apart for them, and from the Amphibia upward in the animal scale this dorsal part of the thalamus assumed increasingly greater importance. This part is termed by Edinger the neothalamus, and makes up by far the larger part of the thalamus in the human and all other mammalian brains. It occupies the dorso-lateral part of the thalamus proper and comprises most of the great thalamic

[1] The paragraphs which follow (pp. 343–349) are reproduced with slight modification from The Journal of Animal Behavior, vol. iii, 1913, pp. 228–236.

nuclei (lateral and ventral nuclei, pulvinar and lateral and medial geniculate bodies). The primitive intrinsic reflex thalamic apparatus in man is a relatively unimportant area of medial gray matter and the subthalamic region (corpus Luysii, lattice nucleus, etc., not to be confused with the hypothalamus which lies farther down in the tuber cinereum and mammillary bodies).

The neothalamus, accordingly, serves as a sort of vestibule to the cortex, every afferent impulse from the sensory centers (except the olfactory system) being here interrupted by a synapse and opportunity offered for a wide range of subcortical associations. The olfactory cortex (hippocampal formation) has a similar relation to subcortical correlation centers in the olfactory area in the anterior perforated space, septum, etc.

From these anatomical considerations it follows that no simple sensory impulse can, under ordinary circumstances, reach the cerebral cortex without first being influenced by subcortical correlation centers, within which complex reflex combinations may be effected and various automatisms set off in accordance with their preformed structure. These subcortical systems are to some extent modifiable by racial and individual experience, but their reactions are chiefly of the invariable or stereotyped character, with a relatively limited range of possible reaction types for any given stimulus complex.

It is shown by the lower vertebrates which lack the cerebral cortex that these subcortical mechanisms are adequate for all of the ordinary simple processes of life, including some degree of associative memory. But here, when emergencies arise which involve situations too complex to be resolved by these mechanisms, the animal will pay the inevitable penalty of failure—perhaps the loss of his dinner, or even of his life.

In the higher mammals with well-developed cortex the reflexes and simple associations are likewise performed in the main by the subcortical apparatus, but the inadequacy of this apparatus in any particular situation presents not the certainty of failure, but rather a dilemma. The rapid, preformed reflex mechanisms fail to give relief, or perhaps the situation presents so many complex sensory excitations as to cause mutual interference and inhibition of all reaction. There is a stasis in the subcortical centers. Meanwhile the higher neural resistance of the cortical pathways has been overcome by summation of stimuli and the cortex is excited to function. Here is a mechanism adapted, not for a limited number of predetermined and immediate responses, but for a much greater range of combination of the afferent impressions with each other and with memory vestiges of previous reactions and a much larger range of possible modes of response to any given set of afferent impressions. By a process of trial and error, perhaps, the elements necessary to effect the adaptive response may be assembled and the problem solved.

It is evident here that the physiological factors in the dilemma or problem as this is presented to the cortex are by no means simple sensory impressions, but definitely organized systems of neural discharge, each of which is a physiological resultant of the reflexes, automatisms, impulses, and inhibitions characteristic of its appropriate subcortical centers. The precise form which these subcortical combinations will assume in response to any particular excitation is in large measure determined by the structural connections of these centers *inter se*. And the pattern of these connections is tolerably uniform for all members of any animal race or species. This implies that it is hereditary and innate. This is the underlying basis of instinct.

The connections between the cortical centers, on the other hand, are much less definitely laid down in the hereditary pattern. The details of the definitive association pattern of any individual are to a greater degree fixed by his particular experience. This is the basis of docility and the individually modifiable or intelligent types of behavior. The typical cortical activities, even when physiologically considered, are far removed indeed from those of the brain stem.

It should be emphasized, however, that the differences between the cortex and the lower centers of the brain stem, so far as these can be deduced from a study of structure and from physiological experiment, are relative and not absolute. Indeed, the general pattern of the regional localization of the cortex itself is innate, and in adult life the cortex has acquired many more characteristics similar to those of the brain stem, with its own systems of acquired automatisms and habitually fixed types of response. The larger association centers retain their plasticity longest, but ultimately these also cease to exhibit new types of correlation, and this marks the onset of senility.

The relations of the cerebral cortex to the cerebellar cortex and the brain stem have been compared (p. 216) to those of an enlarged judicial branch of the central government charged with the duty of interpreting the decrees of the lower legislative centers and dominating the administrative machinery, and with the additional power of shaping the general policy of the government.

Dewey's stimulating analysis[1] of the reflex arc concept or, as he prefers to say, the organic circuit concept implies that the synthesis of the elements of a complex chain reflex into an organic unity is the essential prerequisite of that apperceptive process which will make the total experience of value for future discriminative responses—for learning by experience. This, which is true in the individual learning process, is also true phylogenetically. The correlation centers (and their capacity for the preservation of vestiges of past reactions) are the organic mechanism for this synthesis. They make it possible that a new stimulus may be reacted to, not as a detached element, but as a component of a complex series of past and present adjustments, to which it is assimilated in the association centers—apperception. This assimilation or apperceptive process is an integral part of the receptor process in the higher centers, giving the quale to the idea of the exciting object. Contemporaneously with this stimulus-apperception process we have an apperception-response-activity giving the object- or purpose-idea, so that the entire reaction is to be regarded as stimulus-apperception-response, as a functional unity rather than as a sequence: stimulus>apperception>response.

Dewey's organic circuit concept is elaborated in terms of psychology. Let us see how it may be applied to biological behavior.

The simple reflex is commonly regarded as a causal sequence: given the gun (a physiologically adaptive structure), load the gun (the constructive metabolic process), aim, pull the trigger (application of the stimulus), discharge the projectile (physiological response), hit the mark (satisfaction of the organic need). All of the factors may be related as members of a simple mechanical causal sequence except the aim. For this in our illus-

[1] The Reflex Arc Concept in Psychology, Psych. Rev., vol. iii, p. 357, 1893. See also Dewey's later statement in Jour. Philos., Psych., and Sci. Methods, vol. ix, Nov., 1912, pp. 664–668, especially the footnote on p. 667.

tration a glance backward is necessary. An adaptive simple reflex is adaptive because of a pre-established series of functional sequences which have been biologically determined by natural selection or some other evolutionary process. This gives the reaction a definite aim or objective purpose. In short, the aim, like the gun, is provided by biological evolution, and the whole process is implicit in the structure-function organization which is characteristic of the species and whose nature and origin we need not here further inquire into.

Now, passing to the more complex instinctive reactions, so far as these are unconscious automatisms, they may be elaborations of chain reflexes of the type discussed above (p. 64). But the *aim* (biological purpose) is so inwrought into the course of the process that it cannot be dissociated. Each step is an integral part of a unitary adaptive process to serve a definite biological *end*, and the animal's motor acts are not satisfying to him unless they follow this predetermined sequence, though he himself may have no clear idea of the aim.

These reactions are typical organic circuits. The cycle in some of the instincts of the deferred type comprises the whole life of the individual. In other cases the cycle is annual (as in bird migrations, etc.), diurnal, or linked up with definite physiological rhythms (*e. g.*, the nidification of birds as described by F. H. Herrick, see p. 64). In still other cases there is no apparent simple rhythm. But always the process is not a simple sequence of distinct elements, but rather a series of reactions, each of which is shaped by the interactions of external stimuli and a preformed or innate structure which has been adapted by biological factors to modify the response to the stimuli in accordance with a purpose, which from the standpoint of an outside observer is teleological, *i. e.*, adapted to conserve the welfare of the species.

Every intelligently directed response to external stimulation involves a large measure of highly complex unconscious cerebration of this type; and it is possible to describe with considerable precision the mechanisms of the subcortical activities involved in many of those organic circuits which are commonly regarded as typically cortical.

Much of that which goes in psychological literature under such contradictory terms as unconscious mind or subconscious mind is, in reality, the subcortical elaboration of types of action system which ordinarily do not involve the cortex at all, but which upon occasion may be linked up with cortical associational processes and then come into consciousness in such a form as to suggest to introspection that they are all of a piece with the conscious process with which they are related. In fact, within the cortex itself there are doubtless many routine activities which do not ordinarily come into consciousness, particularly of the sort known as acquired automatisms or lapsed intelligence; and these, though of quite different origin from the innate instinctive systems, cannot easily be distinguished from them in the form in which they are experienced in the adult.

In the organic circuit as defined by Dewey the process is considered as a whole, so that the response is conceived as logically implicit in the stimulus. The motor reaction, he says, is not merely *to* the stimulus; it is *into* the stimulus. "It occurs to change the sound, to get rid of it. What we have is a circuit, not an arc, or broken segment of a circle. This circuit is more truly termed organic than reflex, because the motor response determines the stimulus just as truly as sensory stimulus determines movement." This notion, which is difficult for the practical

scientific mind to understand, is considerably clarified by some neurological considerations.

From the standpoint of the cerebral cortex considered as an essential part of the mechanism of higher conscious acts, every afferent stimulus, as we have seen, is to some extent affected by its passage through various subcortical correlation centers (*i. e.*, it carries a quale of central origin). But this same afferent impulse in its passage through the spinal cord and brain stem may, before reaching the cortex, discharge collateral impulses

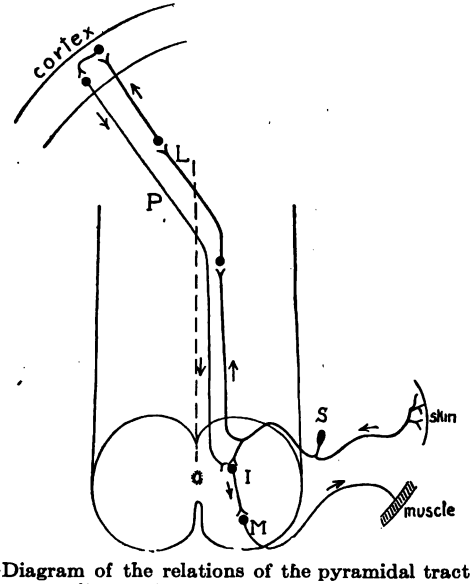

Fig. 140.—Diagram of the relations of the pyramidal tract in a rabbit or similar lower mammalian brain. Sensory stimuli enter the spinal cord from the skin through the peripheral sensory neuron, *S*, and ascend to the cerebral cortex through the lemniscus, *L*. The descending pyramidal tract, *P*, lies in the dorsal funiculus of the spinal cord. Its intercalary neuron, *I*, may be stimulated by both the peripheral neuron, *S*, and by the pyramidal tract, *P*. It discharges upon the peripheral motor neuron, *M*.

into the lower centers of reflex coördination, from which incipient (or even actually consummated) motor responses are discharged previous to the cortical reaction. These motor discharges may, through the "back stroke" action, in turn exert an influence upon the slower cortical reaction. Thus the lower reflex response may in a literal physiological sense act *into* the cortical stimulus complex and become an integral part of it.

But there is another aspect of the problem which has recently been brought to our notice by Kappers.[1] It is a well-known fact, which is not

[1] KAPPERS, C. U. ARIËNS. Ueber die Bildung von Faserverbindungen auf Grund von simultanen und sukzessiven Reizen. Bericht über den

often taken account of in this connection, that the descending cortical paths (pyramidal tracts) do not typically end directly upon the peripheral motor neurons whose functions they excite, but rather upon intercalary neurons which lie in the reticular formation or even in the adjacent sensory centers. These intercalary neurons, in turn, excite the peripheral motor neurons. The same intercalary neuron which receives the terminals of the pyramidal tract also receives collaterals from the peripheral sensory neurons of its own segment (Fig. 140). This arrangement is the explanation of the fact that the pyramidal tract fibers descend through the human spinal cord for the most part in the dorso-lateral region, not in the ventral funiculus like most other motor tracts. In most lower mammals the pyramidal tract actually descends within the dorsal funiculus in the closest possible association with the peripheral sensory fibers, and this arrangement is clearly the primitive relation of the descending cortical pathway.

Accordingly, stimulation of the skin of the body excites a dorsal spinal root fiber which ascends toward the cortex within the spinal cord and also gives collateral branches to intercalary neurons of the spinal cord itself. The latter neurons may excite motor elements of the spinal cord to an immediate reflex response which is well under way before the cortical return motor impulse gets back to the spinal cord and discharges into these same intercalary neurons which are already under sensory stimulation directly from the periphery. The effect of this arrangement is that the central motor path during function is under the influence of sensory stimulation at both ends, and is not, as commonly described, under simple sensory stimulation at the cortical end and purely emissive in function at the spinal end.

Viewed from the standpoint of cerebral dynamics, the exact physiological effect of the discharge of a central motor bundle such as the pyramidal tract will be dependent upon the combined action of the sensory stimulation at the cortical end and the state of sensory excitation at the spinal end, as well as upon the resistance of the motor apparatus itself.

We saw in a previous paragraph how the simple reflexes of the spinal cord may become factors in the stimulus complex of the cortex. Here we find, conversely, that the efferent cortical discharge may become a factor in the local reflex stimulation of a motor spinal neuron. From both standpoints Dewey's conception of the unitary nature of the organic circuit, as contrasted with the classical reflex arc concept, receives strong support.

The thalamic correlation centers probably serve as the organs *par excellence* where are elaborated those organic circuits which give to the higher apperceptive processes of the cortex that quale to which Dewey refers. The origin of this quale is to be sought partly in the subcortical assimilation of a present stimulus complex to the pre-existing organic circuits structurally laid down in the reflex mechanism, and partly in an affective quality pertaining to the several organic circuits involved in the reaction. This affective quality may be innate or it may have been

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III Kongress für experimentelle Psychologie in Frankfurt a. Main, 1908. Also Weitere Mitteilungen über Neurobiotaxis. Folia Neuro-Biologica, Bd. I, No. 4, April, 1908, pp. 507–532.

See also DEARBORN, G. V. N. Kinesthesia and the Intelligent Will, Amer. Jour. of Psychol., vol. xxiv, 1913, pp. 204–255.

acquired by experience of the results of previous reactions of the sort in question.

Head and Holmes have brought forward some very interesting evidence that not only the affective quale of sensations but also the emotional life in general is functionally related to the primitive intrinsic nuclei of the thalamus, rather than to cortical activity (see p. 284). And certainly there is much evidence in the behavior of lower animals, especially birds, that a high degree of emotional activity is possible where the basal centers are highly elaborated but the cerebral cortex is small and very simply organized.

From all of these considerations it seems probable that the functions of the higher association centers of the cerebral cortex do not consist of the elaboration of crude sensory data or of any similar elements, but rather of the assembling and integration of highly elaborated subcortical organic circuits which in the aggregate make up the greater part of the reflex and instinctive life of the species.

The functions of the cerebral cortex fall into two great groups: (1) Correlations of great complexity, *i. e.*, with many diverse factors. This is of no practical value without capacity for choice between many possible different reactions to the situation. This "switch-board" type of function is simply a higher elaboration of the physiological patterns of the lower correlation centers. (2) Retentiveness of past individual impressions in such form as to permit of subsequent recall and incorporation into new stimulus complexes. This mnemonic function is simply a higher elaboration of primitive protoplasmic "organic memory" or individual modifiability. The mechanism of the first group of functions may be largely innate and heritable; that of the second is necessarily individually acquired. These two functions lie at the basis of all *mind*.

The normal newborn child brings into the world an inherited form of body and brain and a complex web of nerve-cells and nerve-fibers which provide a fixed mechanism, common except for minor variations to all members of the race alike, for the performance of the reflex and instinctive actions. The pattern of this hereditary fabric can be changed only very slowly by the agency of selective matings and other strictly biological factors or by degenerations of a distinctly pathological sort. It is thus manifest that the improvement of the racial stock of normal individuals by the practice of eugenics must necessarily be very slow, though the improvement of defective or pathological strains by selective matings so as to breed out

the objectionable characteristics is fortunately in most cases more readily accomplished.

But in addition to this hereditary organization the newborn child possesses the large association centers of the brain with their vast and undetermined potencies, the exact form of whose internal organization is not wholly laid down at birth, but is in part shaped by each individual separately during the course of the growth period by the processes of education to which he is subjected, that is, by his experience. This capacity for individuality in development, this ability to profit by experience, this docility, is man's most distinctive and valuable characteristic. And since the form which this modifiable tissue will take is determined by the environing influences to which the child is subjected, and since these influences are largely under social control, it follows that human culture can advance by leaps and bounds wherever a high level of community life and educational ideals is maintained.

So well have we learned the lesson that the child brings with him into the world no *mental* endowments ready-made—no knowledge, no ideas, no morals—but that these have to be developed anew in each generation under the guiding hand of education, that we devote one-third of the expected span of life of our most promising youth to the educational training necessary to ensure the highest possible development of the latent cultural capacities of these association centers of the cerebral cortex.

But we have often been blind to the other side of the picture. We have seen above that the adult cortex cannot function save through the reflex machinery of the brain stem, and it must not be forgotten in our pedagogy that this relation holds in a much more vital and significant sense in the formative years of the child. It is true that the child is born with no mental endowments; but how rich is his inheritance in other respects! He has an immense capital of preformed and innate ability which takes the form of physiological vigor and instinctive and impulsive actions, performed for the most part automatically and unconsciously. This so-called lower or animal nature is ever present with us. In infancy it is dominant; childhood is a period of storm and stress, seeking an equilibrium between the

stereotyped but powerful impulsive forces and the controls of the nascent intellectual and moral nature; and in mature years one's value in his social community life is measured by the resultant outcome of this great struggle in childhood and adolescence. This struggle is education.

The answer to the riddle of life, however, lies not in a successful attack upon the native innate endowments of the child. No, that would be unbiological and wasteful, for our world of ideas and morals is no artificial world within the cosmos, but it is a natural growth, which is as truly a part of the cosmic process as are "ape and tiger methods" of evolution. No higher association center of the human brain can function except upon materials of experience furnished to it through the despised lower centers of the reflex type. So also, no high intellectual, esthetic, or moral culture can be reached save as it is built upon the foundation of innate capacities and impulses.

We are gradually learning through the kindergarten that the most economical way to lead a child into the realm of learning is not to stamp out all of his natural interests and shut him up with his face to the wall, while he learns by rote an a-b-c lesson which is neither interesting nor useful. On the contrary, we accept as given his native impulses and automatisms, his spontaneous interests and his overproduction of useless movements, and we use these as the capital with which we set the youngsters up in the serious business of the acquisition of culture. But how does it happen that we make so small use of the principles here learned in the later years of the child's schooling?

Not all of the instincts with which man is by nature endowed come into function in a sucking babe or a kindergarten pupil. Childish curiosity is our strongest ally, if only we can use it wisely, throughout the whole of the educational career from infancy to the graduate school. Anger is a mighty passion in childhood. It is not wise to eradicate it altogether; rather keep it, though under curb, for there are times when real abuses arise which require that the man know how to hit and to hit hard. And so with the instincts of self-preservation, of fear, of sex—these all have their parts to play in the nobler works of life and are by no means to be eradicated. The ascetic ideal of mortification of the flesh as a means of grace is

fundamentally wrong in principle. Our case calls for no blind, indiscriminate attack upon the world and the flesh, but rather the subjugation and discipline of these, so that we may use them effectively in our attack upon the devil.

Conflict is inherent in the cosmic process, at least in the biological realm, from beginning to end. There is the struggle for physical existence among the animals. And even in the lower ranks of life there arises also the struggle within the individual between stereotyped innate tendencies or instincts and individually acquired experience. This is clearly shown by experiments on animals as low down as the Protozoa. And out of this inner conflict or dilemma intelligence was born. With the gradual emergence of self-consciousness in this process arises the eternal struggle with self, that conflict which leads to the bitter cry, "When I would do good evil is present with me." Conflict, then, lies at the basis of all evolution, and the factors of social and even of moral evolution can be traced downward throughout the cosmic process.

The social and ethical standards, therefore, have not arisen in opposition to the evolutionary process as seen in the brute creation, but within that process. And our immediate educational problem is the elaboration of a practicable system of public instruction which can use to the full the enormous dynamic energy in the hereditary impulsive and instinctive endowment of the child, and build upon this, in the form best suited to the respective capacities of all the separate individuals, a properly ordered sequence of studies which will develop the latent capacities of each pupil and ensure a vital balance between the strong blind impulse of the innate nature and the acquired intellectual, esthetic, and moral control.

And herein lies the solution of the problem of human freedom, so far as this rests within our own control. The limits of one's powers and the range within which his freedom of action is circumscribed are in part determined by his hereditary endowments and by environmental influences over which he has no control. These are decreed to him by his fate, and the innate organization of the nervous system is the chief instrument of this fate. But man differs from the brute creation chiefly in that he can more completely control his own environment and

thereby to that extent take his fate into his own hands; in other words, he can enrich his own experience along lines of his own selection. To some extent each individual can do this for himself through self-culture; but to ensure the best results of such efforts there must be a social control of the environment as a whole by concerted community action. Individual freedom of action can, therefore, attain its highest efficiency only through a certain amount of voluntary renunciation of the selfish interests where these conflict with community welfare. Ethical ideals and altruism are as truly evolutionary factors in human societies as are the elemental laws of self-preservation and propagation of the species.[1]

To return now to the developing nervous system, we note that the educational period is limited to the age during which the association centers, whose form is not predetermined in heredity, remain plastic and capable of modification under environmental influence. Ultimately even the cerebral cortex matures and loses its power of reacting except in fixed modes. Its unspecialized tissue—originally a diffuse and equipotential nervous meshwork—becomes differentiated along definite lines and the fundamental pattern becomes more or less rigid. The docile period is past, and though the man may continue to improve in the technic of his performance, he can no longer do creative work. He is apt to say, "The dog is too old to learn new tricks." Whether this process occurs at the age of twenty or eighty years, it is the beginning of senility. And, alas, that this coagulation of the mental powers often takes place so early! Many a boy's brains are curdled and squeezed into traditional artificial molds before he leaves the grades at school. His education is complete and senile sclerosis of the

[1] In this connection reference may be made to three very interesting public addresses recently delivered before the American Society of Naturalists:

JENNINGS, H. S. 1911. Heredity and Personality, Science, N. S., vol. xxxiv, pp. 902–910.

CONKLIN, EDWIN G. 1913. Heredity and Responsibility, Science, N. S., vol. xxxvii, pp. 46–54. (See also the last chapter of this author's book on Heredity and Environment, Princeton, 1915.)

PARKER, G. H. 1915. The Value of Zoology to Humanity: The Eugenics Movement as a Public Service, Science, N. S., vol. xli, No. 1053, pp. 342–347.

mind has begun by the time he has learned his trade. For how many such disasters our brick-yard methods in the public schools are responsible is a question of lively interest.

We who seek to enter into the kingdom of knowledge and to continue to advance therein must not only become as little children, but we must learn to *continue so.* The problem of scientific pedagogy, then, is essentially this: to prolong the plasticity of childhood, or otherwise expressed, to reduce the interval between the first childhood and the second childhood to as small dimensions as possible.

INDEX AND GLOSSARY

The references are, in all cases, to pages. Numbers referring to pages upon which the item is figured are printed in **black-faced type**. Authors' names are printed in SMALL CAPITALS. Brief definitions of some of the more commonly used technical terms are included in this Index; for fuller descriptions consult the pages cited. Terms which are defined in this Glossary are printed in **black-faced type**. The names of fiber tracts, in general, define their connections, the first part of the compound word indicating the nucleus of origin and the last part the terminal nucleus (see pages 117, 138). To facilitate cross-reference, the key-word of a polynomial term is capitalized wherever it occurs in this Index and Glossary.

Tables of synonyms of most anatomical names will be found in the works by KRAUSE and EYCLESHYMER, cited on page 134.

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Affection, affective experience, affective tone, pleasure-pain, emotions, and allied phenomena; cf. Feeling tone and Pain, 95, 182, 270, 279–292, 348

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Agraphia, loss of the power to write correctly, 328

Agreeable and disagreeable. See Affection.

Ala cinerea (vagal eminence, eminentia vagi, trigonum vagi), an eminence in the floor of the fourth ventricle formed by the dorsal Nucleus of the vagus, **168, 170, 178, 263, 273**

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Apoplexy, 329
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Aqueduct of Sylvius (itèr, optocœle, mesocœle), the ventricle of the midbrain, **65**, 129, 175, **176**
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Arbor vitæ, the tree-like appearance of the white matter of the cerebellum in section, 213
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Archipallium, the olfactory cerebral cortex, including the **Hippocampus** and the **Gyrus hippocampi** (in part), 243, **248**, 320
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acoustico-lateral (in fishes = tuberculum acusticum), **119**, **120**, 155, **163**, **166**, 207, **225**
cortical, as used in this work, is a part of the cerebral cortex which can be differentiated from its neighbors structurally by the arrangement of its cells and fibers (sometimes termed field); cf. **Center, cortical**, **307**, 308, 322, 323, **324**
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olfactoria, the region containing the secondary olfactory centers, divided into anterior, medial, intermediate, and lateral **olfactory Nuclei**, **180**, 242, **244**, **245**, **246**
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somatic, a small region in the fish brain from which the **Neopallium** and **Corpus striatum** were developed.
striata, that part of the occipital lobe of the cerebral cortex containing the **Line of Gennari**; the visual center, **299**, 320
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Aula, the anterior end of the third ventricle where it communicates with the lateral ventricles by way of the interventricular **Foramina.**
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Axis-cylinder, the central protoplasmic strand of a nerve-fiber; part of the **Axon**, 41

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Back-stroke, the influence which a peripheral organ of response exerts back upon the center from which the response was excited; a form of **chain Reflex**; cf. **Reflex circuit,** 291, 347
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Behavior, invariable, activities whose character is determined by innate structure, typified by reflex and instinctive actions, 32, 72, 83, 84, 199, 294, 338–341
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B. N. A. See Basle nomina anatomica.
Body of cell. See **Cell body.**
chromophilic. See **Substance, chromophilic.**
of fornix. See **Fornix body.**
geniculate, lateral (corpus geniculatum laterale, external geniculate body), a visual center in the Thalamus, 164, **177, 178,** 179, 183, 234, **236,** 238, 320, 344
geniculate, medial (corpus geniculatum mediale, internal geniculate body), an auditory center in the Thalamus, **123, 127, 168,** 171, **177, 178,** 180, 183, **204, 226,** 227, **344**
habenular. See **Habenula.**
of LUYS, 183, 344
mammillary (corpus mamillare, corpus candicans), one of a pair of eminences at the posterior end of the **Tuber cinereum** in the **Hypothalamus**; an olfactory center, **129,** 179, **180, 181,** 183, **236, 246,** 344
of NISSL. See **Substance, chromophilic.**
pineal (corpus pineale, pineal gland, epiphysis, conarium), a glandular outgrowth from the **Epithalamus**; in some lower vertebrates it takes the form of a median dorsal eye. See **Parietal eye, 118, 127, 128, 177, 178,** 183, 238
pituitary. See **Hypophysis.**
quadrigeminal. See **Corpora quadrigemina.**
restiform. See **Corpus restiforme.**
striate. See **Corpus striatum.**
tigroid. See **Substance, chromophilic.**
trapezoid (corpus trapezoideum), transverse decussating fibers in the ventral part of the medulla oblongata which connect the auditory nuclei of one side with the **lateral Lemniscus** of the other side, **52, 226**

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conjunctivum (prepeduncle), the superior or anterior peduncle of the cerebellum; cf. **Peduncle, cerebellar, 123, 141, 173, 177, 194, 206**
pontis (medipeduncle, processus cerebelli ad pontem), the middle peduncle of the cerebellum; cf. **Peduncle, cerebellar, 123, 130, 173, 177, 206,** 207, 215
quadrigeminum inferius (brachium of colliculus inferior), a ridge on the **Corpora quadrigemina** formed by fibers from the **Colliculus inferior** to the medial **geniculate Body, 123, 176, 177,** 204
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new. See **Neëncephalon.**
nomenclature of. See Nervous system, nomenclature of.
old. See **Palæëncephalon.**
reflexes of. See Reflexes of brain stem.
stem, all of the brain except the cerebellum and the cerebral cortex and their dependencies, *i. e.*, the **Segmental apparatus,** 121, **123,** 131, **178,** 199, **204,** 205, 216
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Bulb (bulbus), any bulblike structure; specifically the **Medulla oblongata,** as in bulbar paralysis, tractus bulbo-spinalis.
olfactory, a protuberance from the cerebral hemisphere containing the primary olfactory center, **118, 119, 120, 129, 180,** 241, **243, 244, 245, 246, 295**
Bulbar formation. See **Formatio bulbaris.**
Bundle. See **Tract** and **Fasciculus.**
basis, fundamental, or ground. See **Fasciculus proprius.**
longitudinal medial. See **Fasciculus longitudinalis medialis.**
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Cajal, commissural nucleus of. See Nucleus, commissural, of Cajal.
Calcar avis (hippocampus minor), a projection into the posterior horn of the lateral ventricle formed by the calcarine fissure.
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Canal, central (canalis centralis), the ventricle of the spinal cord, 136, 139
lateral line. See **Organs, lateral line.**

Canal, neural, the lumen of the embryonic **Neural tube**; also applied to the **spinal Canal** of the vertebral column.
semicircular (ductus semicircularis). See also Vestibular apparatus, 93, **118, 119,** 202, **203,** 205, **219, 220, 225, 226**
spinal, the canal in the vertebral column containing the **Spinal cord.**
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internal (capsula interna), a strong band of nerve-fibers passing through the **Corpus striatum, 123,** 180, **181, 184,** 186, **190, 194, 236,** 283, 298, 323
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Cat, nervous system of, **95,** 281
Catfish, nerves of, **275**
Cauda equina, a bundle of elongated spinal nerve roots arising from the lumbar and sacral segments of the spinal cord.
Caudal, pertaining to the tail, or directed toward the tail end of the body, as opposed to **cephalic,** 125
Cavum septi pellucidi (fifth ventricle, pseudocœle), the space enclosed between the **Septa pellucida** of the two cerebral hemispheres; not a true **ventricle.**
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neuroglia. See **Neuroglia.**
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Cellulipetal, conducting toward the **Cell body,** applied to the processes of a **neuron.**
Center (centrum), a collection of nerve cells concerned with a particular function, 26, 116, 117, 199, 339
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cortical, a part of the cerebral cortex which can be differentiated functionally from its neighbors; cf. **Area, cortical.** These centers are sometimes called areas, fields, spheres, or zones, 308, **317, 318,** 325
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Chromatin, a nucleoprotein substance found in the cell nucleus, 105
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Chromophilic bodies, granules, or substance. See **Substance, chromophilic.**
Ciliary process. See Process, ciliary.
Cingulum, an association tract of the cerebral hemisphere lying under the Gyrus cinguli, **298**
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Circuit, organic. See **Reflex circuit.**
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Claustrum, a thin band of gray matter between the external **Capsule** and the cortex of the island of REIL, or **Insula.**
Clava, an eminence on the dorsal surface of the lower end of the medulla oblongata produced by the nucleus of the **Fasciculus gracilis, 140, 194, 206**
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fundamental. See **Fasciculus proprius.**
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gray (columna grisea), one of the longitudinal columns of neurones which make up the gray matter of the spinal cord. There are three columns: (1) **dorsal** (posterior), (2) **ventral** (anterior), and (3) **lateral** (middle or intermediate). These columns were formerly called horns (cornua); cf. also **Funiculus, 136,** 137, **138, 139,** 148, **164, 165**
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of hippocampus (commissura hippocampi, commissura fornicis), fibers connecting the **Hippocampi** of the two sides through the **Fornix body, 184, 246,** 296
inferior. See **Commissure, postoptic.**
of MEYNERT. See **Commissure, postoptic.**
middle. See **Massa intermedia.**
mollis. See **Massa intermedia.**
posterior (commissura posterior), fibers passing transversely through the anterior end of the roof of the midbrain, **177, 246**
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Coördination, the combination of nervous impulses in motor centers to ensure the coöperation of the appropriate muscles in a reaction, 36, 71, 199
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basilaris of cochlea, **221**
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Crus, a stalk or peduncle, applied to compact masses of fibers which connect different parts of the brain; cf. **Peduncle.**
commune, of internal ear, **220**
fornicis. See **Fornix, crus of.**
olfactoria, the stalk or peduncle of the **Olfactory bulb.**
Crusta. See **Basis pedunculi.**
Crustaceans, nervous system of, 30
Culmen monticuli, **211, 212**
Cuneus, a wedge-shaped gyrus on the medial face of the posterior pole of the cerebral hemisphere receiving visual projection fibers, **128, 184,** 185, **236, 310**
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Cup, optic. See also **Vesicle, optic, 230**
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Current, action, 102
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CYON, nerve of, 264
Cytoplasm, all protoplasm of a cell exclusive of that in the nucleus, 40, 102, 105, 108

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Decussation (decussatio), a band of fibers crossing the median plane of the central nervous system and connecting unlike centers of the two sides; many decussations are called **commissures.**
of FOREL. See Decussation, tegmental, ventral.
fountain. See Decussation, tegmental, dorsal.
of MEYNERT. See Decussation, tegmental, dorsal.
optic. See **Chiasma, optic.**
of pyramids, 141
tegmental, dorsal (MEYNERT'S decussation, fountain decussation), 142, **176**
ventral (FOREL'S decussation), 141, **176**
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Dendrite, a process of a **Neuron** which conducts toward the cell body, 40, **41, 42, 43, 45, 47, 48,** 102, 108, 110, 111
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Diaschisis, a transitory defect of function due to disturbance of cortical equilibrium, 329
Diencephalon (betweenbrain, thalamencephalon), the brain region lying between **Mesencephalon** and **Telencephalon;** sometimes called **Thalamus** or **Optic thalamus,** but properly divided into **Thalamus, Epithalamus,** and **Hypothalamus, 124, 126–128,** 131, 132, 176–183
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Dorsal, on the back side of the body, termed **posterior** in the B. N. A. lists, 125
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semicircularis. See Canal, semicircular, and Vestibular apparatus.
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Ear. See Auditory apparatus and Vestibular apparatus.
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Ectoderm (epiblast), the outer germ layer of the embryo, from which the epidermis and the **Neural tube** develop, **230**
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Edinger-Westphal, nucleus of (the visceral efferent nucleus of the III nerve; cf. Nucleus of oculomotor nerve).
Education, 33, 349–354
Effector, an organ of response, **27,** 98
Efferent, conducting away from a center, 27, 44, 116, 136, 147
Electric excitability of nervous tissues, 316, 318, 321
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Embryology of nervous system. See Nervous system, embryology of.
Eminentia abducentis. See **Colliculus facialis.**
facialis. See **Colliculus facialis.**
Eminentia hypoglossi. See **Trigonum hypoglossi.**
medialis (eminentia teres), a medial longitudinal ridge in the floor of the fourth ventricle; an enlarged portion is the **Colliculus facialis.**
Eminentia teres. See **Eminentia medialis.**
vagi. See **Ala cinerea.**
Emotion. See Affection.
Empis stercorea, nervous system of, **31**
Encephalon, the brain, 125
End-nucleus. See **Nucleus, terminal.**
End-organ, the peripheral apparatus related to a nerve; a **Receptor** or **Effector,** 27, 74, 84–99
End-plate, motor; the **terminal arborization** of a motor axon upon a muscle-fiber, **41,** 98, 108
Endolymph, 220
Endyma. See **Ependyma.**
Engram, 331
Environment, 17, 18, 74, 350
Epencephalon, the cerebellum.
Ependyma (endyma), the lining membrane of the ventricles of the brain, derived from the original epithelium of the **Neural tube,** 39
Epiblast. See **Ectoderm.**
Epicritic sensibility, a highly refined type of cutaneous sensibility, especially on hairless parts, 89, 90
Epiglottis, organs of taste upon, 161, 274
Epinephrin. See Adrenalin.
Epiphysis. See **Body, pineal.**
Epithalamus, the dorsal subdivision of the **Diencephalon,** containing the **pineal Body** and the **Habenula,** an important olfactory correlation center, **119, 120, 127, 128,** 129, 131, **177, 178, 180,** 182, **246,** 247, 249
Epithelium, a thin sheet of cells, 25
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electric. See Electric excitability of nervous tissues.
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parietal. See **Parietal eye.**
pineal. See **Parietal eye.**

Face brain, 131
Faculties, mental, 315, 321, 326
Falx cerebri, a longitudinal fold of **Dura mater** which extends between the cerebral hemispheres in the longitudinal fissure, 132
Fascia dentata. See **Gyrus dentatus.**
Fasciculus, a bundle of nerve-fibers not necessarily of similar functional connections. The term is often used, however, as a synonym for **Tract,** 138
antero-lateralis superficialis (of GOWERS). See Fasciculus ventro-lateralis superficialis.
Fasciculus cerebello-spinalis. See Tract, spino-cerebellar.
cerebro-spinalis. See Tract, **cortico-spinal.**
communis, a name formerly applied to the **Fasciculus solitarius** in lower vertebrate brains.
cuneatus (column of BURDACH), the lateral portion of the **dorsal funiculus** of the spinal cord, 138, **140, 149**, 193, **194**
nucleus of. See **Tuberculum cuneatum.**
dorso-lateralis (LISSAUER'S zone, LISSAUER'S tract), **140**, 265, 283
of GOWERS. See Fasciculus ventro-lateralis superficialis.
gracilis (column of GOLL), the medial portion of the **dorsal Funiculus** of the spinal cord, 138, **140, 149, 177**, 193, **194**
nucleus of. See **Clava.**
interfascicularis (comma tract, tract of SCHULTZE), **140**, 142
longitudinalis inferior of cerebral hemisphere, **248, 298**
longitudinalis medialis (medial longitudinal bundle, posterior longitudinal bundle, fasciculus longitudinalis posterior or dorsalis), a bundle of motor coordination fibers running through the brain stem, 142, **169, 170, 176, 194**, 199, **204, 226**, 237
longitudinalis superior of cerebral hemisphere, **298**
marginalis ventralis, 142
of MEYNERT. See Tract, habenulo-peduncular.
occipito-frontalis inferior of cerebral hemisphere, **298**
proprius of cerebral hemisphere. See **Fibers, arcuate** (1).
proprius of spinal cord (fundamental columns, basis bundles, ground bundles), that portion of the white matter of the spinal cord which borders the gray matter and contains correlation fibers; arranged in dorsal, lateral, and ventral subdivisions, 137, **140**, 142, 143, **196**, 199, **281, 282**, 289

Fasciculus retroflexus of MEYNERT. See Tract, habenulo-peduncular.
solitarius (tractus solitarius, solitary bundle, in lower vertebrates often called **Fasciculus communis**), a longitudinal bundle of fibers in the medulla oblongata containing the central courses of the visceral sensory root-fibers of the cranial nerves, **163, 164, 169, 170, 178,** 263, **266**
sulco-marginalis, **140,** 142
thalamo-mamillaris. See Tract, mamillo-thalamic.
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uncinatus of cerebral hemisphere, **298**
ventro-lateralis superficialis (antero-lateral fasciculus, GOWERS' tract), 138, 141
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Fear. See also Affection, 95, 285, 286
Feeble-mindedness. See Idiocy.
Feeding, reflexes of. See Reflexes of feeding.
Feeling (affective). See Affection.
tone. See also Affection, 279, 284, 288–291
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Fiber, or fibers, fibræ. See **Nerve-fiber.**
arcuate, of the cerebral hemisphere, short association fibers connecting neighboring gyri; also called fibræ propriæ and fasciculi proprii, **298,** 321
of the medulla oblongata, decussating fibers lying in a superficial series (external arcuate fibers) and a deep series (internal arcuate fibers), **123, 169**
association; cf. Tract, association, **298,** 305, 321, 327–329
of MÜLLER, 231, **232**
postganglionic. See **Neuron, postganglionic.**
preganglionic. See **Neuron, preganglionic.**
projection. See **Projection fibers.**
propriæ (arcuate fibers of the cerebral hemisphere), **298,** 321
Field, auditory psychic, 320
cortical, a term sometimes used as a synonym of **Center, cortical,** or of **Area, cortical.**
visual psychic, 320
Fila olfactoria, the filaments of which the olfactory nerve is composed, 97, 160, **244**
Fillet. See **Lemniscus.**
Filum terminale (terminal filament), the slender caudal termination of the spinal cord, **115**
Fimbria, a band of fibers which borders the **Hippocampus** and joins the **Fornix, 180, 246, 248,** 296
Final common path, **61,** 65, 107, 288
FISCHER, B., 314, 336
Fishes, nervous system of, 117, **118–120,** 131, 162–167, 181, 196, 199, 207, 224, **225,** 238, 241, 266, 270, **275,** 313, **340**
FISKE, E. W, 13
Fissure (fissura), in the cerebral cortex a deep fold which involves the entire thickness of the brain wall; cf. **Sulcus.** This is the usage of the B. N. A., but fissure and sulcus are often used as synonyms and the B. N. A. is not consistent in this matter.
calcarine, **128**
chorioid, the fold in the posterior-medial wall of the cerebral hemisphere through which the lateral **chorioid Plexus** is invaginated.
dorsal, of spinal cord (dorsal median septum), 138, **139**
ectorhinal. See **Fovea limbica.**
hippocampal, **248**
lateral (fissura lateralis SYLVII, fissure of SYLVIUS), a deep fissure on the lateral surface of the cerebral hemisphere which separates the temporal from the frontal and parietal lobes, **130, 181,** 297
longitudinal, the great fissure between the two cerebral hemispheres, **129,** 296
parieto-occipital, **128, 130**
prima (sulcus primarius), 210, **211, 212**
rhinal. See **Fovea limbica.**
of ROLANDO. See Sulcus centralis.

Fissure secunda, **211, 212**
ventral, of spinal cord, 137, 138, **139**
Fistula, gastric, 271
FLATAU, ED., 14
FLECHSIG, P., 322–324, 336
tract of. See Tract, spino-cerebellar, dorsal.
Flexure, a bending or crumpling of the developing **Neural tube** caused by unequal growth of its parts, as cervical, pontile, mesencephalic, diencephalic, and telencephalic flexures, **124, 126–128**
Flies, nervous system of, **31**
Flocculus, the most lateral lobe of the cerebellum, **177, 210, 211**
FLOURENS, J. P. M., 268
Fluid, cerebro-spinal, a clear liquid filling the ventricles of the brain and spinal cord and subarachnoid space, 133
Folium, one of the leaf-like subdivisions of the cerebellar cortex; these are termed **Gyri** in the B. N. A., 213
vermis, **212**
Foramen interventriculare (foramen of MONRO, porta), the communication between the lateral and the third ventricles, **293**
of Magendie, a medial aperature in the membranous roof of the fourth **Ventricle, 177**
of MONRO. See **Foramen interventriculare.**
Forebrain. See **Prosencephalon.**
FOREL, decussation of. See Decussation, tegmental, ventral.
field of, 183
Formatio bulbaris (bulbar formation), the tissue comprising the primary olfactory center in the olfactory bulb, *i. e.*, the **Glomeruli, mitral Cells,** and **granule Cells, 244,** 246
reticularis (reticular formation, processus reticularis in spinal cord), a mixture of nerve-fibers and cell bodies providing for local reflexes, 69, 137, **139, 140, 167, 170,** 172, **190, 194,** 199, 203, 268, 276, 341, 348
vermicularis, 210
Fornix, a complex fiber system connecting the **Hippocampus** with other parts of the brain, **177, 178, 180, 181, 248**
body (corpus fornicis), the middle part of the **Fornix.**
columns (columnæ fornicis, anterior pillars of fornix), two columnar masses of fibers diverging from the anterior end of the **Fornix body** to descend into the diencephalon, **177, 180, 184, 246,** 249
commissure. See **Commissure of hippocampus.**
crus of (crus fornicis, posterior pillar of fornix), a band of fibers on each side of the brain connecting the posterior part of the **Fornix body** with the **Fimbria.**
longus of FOREL, fibers which perforate the **Corpus callosum** and pass through the **Septum pellucidum.**
FORTUYN, A. B. D., 14, 174
Fossa lateralis (fossa of SYLVIUS), a deeper part of the **Fissura lateralis** containing the **Insula.**
rhomboidal, the floor of the fourth ventricle, **127, 177**
Fovea limbica (sulcus rhinalis, fissura rhinica, fissura rhinalis, fissura ectorhinalis), the sulcus which marks the lateral border of the lateral **Area olfactoria** and **Gyrus hippocampi** or **pyriform Lobe** in the lower mammals.
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Freedom of action, 352
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FRITSCH, G., 316, 336
Frog, cerebral cortex of, 242, **296,** 313
nerve endings in, **96**
reaction time of, 104
reactions of, 66
velocity of nervous transmission in, 103
Funiculus, one of the three principal divisions of white matter on each side of the spinal cord; these funiculi were formerly called **Columns, 138**

Funiculus, dorsal (funiculus dorsalis or posterior, posterior columns), the white matter of the spinal cord included between the dorsal fissure and the dorsal root, **138, 139, 140,** 148, **149, 152, 164, 165,** 193, **194,** 195–199, 348
lateral (funiculus lateralis, lateral columns), the white matter of the spinal cord included between the dorsal and ventral roots, **138**
ventral (funiculus ventralis or anterior, ventral, or anterior columns), the white matter of the spinal cord included between the ventral fissure and the ventral root, **138**

GALL, F. G., 314, 315, 336
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Ganglion, a collection of nerve-cells. In vertebrates the term should be applied only to peripheral cell masses, though sometimes **Nuclei** within the brain are so designated, 116, 117
or **ganglia, basal,** a term sometimes applied to the **Corpus striatum** and other subcortical parts of the cerebral hemisphere.
branchial, of vagus, **163**
cerebro-spinal, development of, 46
cervical, inferior, **253**
middle, **253**
superior, **253,** 263
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of CORTI. See Ganglion, spiral.
of facial nerve. See Ganglion, geniculate.
GASSER'S. See Ganglion, semilunar.
geniculate (ganglion geniculi, the ganglion of the VII cranial or facial nerve), 160, **163, 274, 275**
habenulæ. See **Habenula.**
of insects, 30, **31**
interpedunculare. See **Nucleus, interpeduncular.**
of invertebrates, **29,** 30, **31,** 254
jugular (ganglion jugulare), 161, **163**
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opticum basale. See Nucleus, preoptic.
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petrosal (ganglion petrosum), 161, **274**
of SCARPA. See Ganglion, vestibular.
semilunar (ganglion semilunare, GASSER'S ganglion, the ganglion of the V cranial or trigeminal nerve), **46, 119, 120,** 160, 197, **274**
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spinal, **26,** 46, 116, **135, 136, 137, 144,** 145, **146,** 152, 161, 255, **256**
spiral (ganglion spirale, ganglion of CORTI), 161
submaxillary, 160
superior (ganglion superius of IX cranial nerve), 161
supra-esophageal, **29,** 30
sympathetic, **56, 115,** 117, **135, 136,** 252, **253,** 254–260
prevertebral, sympathetic ganglia of the thorax and abdomen other than those of the **sympathetic Trunk.**
vertebral, the ganglia of the **sympathetic Trunk.**
terminale, 242
of trigeminus. See Ganglion, semilunar.
of vagus. See Ganglion, jugular, and Ganglion nodosum.
of vertebrates, 116
vestibular (ganglion of SCARPA), 161
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GEHUCHTEN, A. VAN, 14, 217, 218
Generative organs. See Sexual organs.
Geniculate body. See **Body, geniculate.**
ganglion. See Ganglion, geniculate.
GENNARI, layer of stripe of. See **Line of Gennari.**
Genu, a knee-shaped bend of an organ, such as the genu of the corpus callosum, of the facial nerve, etc.
of corpus callosum, **128**

Gills, 266, 270
innervation of, **118, 119,** 120, **166,** 275
muscles of, 99, 162
Gland, adrenal. See Gland, suprarenal.
intestinal, 251
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pineal. See **Body, pineal.**
pituitary. See **Hypophysis.**
salivary, innervation of, 156, 160, 161, **168, 170, 257,** 270, **273**
suprarenal, 260, 285, 286
Glia. See **Neuroglia.**
Globus pallidus, a part of the **Nucleus lentiformis,** 185
Glomeruli, olfactory, small globular masses of dense **Neuropil** in the olfactory bulb containing the first synapse in the olfactory pathway, **244, 245**
Glycosuria, 285
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GOLL, column of. See **Fasciculus gracilis.**
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GOWERS, fasciculus of. See Fasciculus ventro-lateralis superficialis.
Gradient, physiological, 25
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Granules. See Cells, granule.
chromophilic, tigroid, of NISSL. See **Substance, chromophilic.**
Gray, central, relatively undifferentiated **gray Matter** which retains its primitive position near the ventricles, 137
Groove, medullary. See **Neural groove.**
neural. See **Neural groove.**
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GUDDEN, commissure of. See **Commissure, postoptic.**
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Gustatory apparatus, 77, 79, **96,** 156, 160, 161, 162, 164, 172, 179, 244, 263, 272–276, 340
Gyrus, one of the convolutions or folds of the cerebral cortex bounded by **Sulci** or **Fissures,** 297
Gyrus angularis, **130**
centralis anterior (precentral gyrus), **130,** 151, 198, **300, 301, 306, 307, 309, 317, 318,** 316–319, **324**
posterior (postcentral gyrus), **130, 307, 308, 317,** 320–322
cinguli, **128, 184**
dentatus (fascia dentata), a subsidiary gyrus of the **Hippocampus, 248**
fornicatus (limbic lobe), the marginal portion of the cerebral cortex on the medial aspect of the hemisphere, including the Gyrus cinguli, Gyrus hippocampi, and others; there is a variety of usage regarding its limits
frontalis inferior, **130, 184,** 328
medius, **130**
superior, **128, 130**
hippocampi, that part of the cerebral cortex which borders the **Hippocampus.** Part of it (the **Uncus**) is **Archipallium;** the remainder is transitional to the **Neopallium.** See **Lobe, pyriform,** 243, **245, 248,** 308, 320
lingualis, **128**
occipitalis lateralis, **130**
olfactorius lateralis. See **Nucleus olfactorius lateralis.**
medialis. See **Area parolfactoria of Broca.**
orbitalis, **130**
postcentral. See Gyrus centralis posterior.
precentral. See Gyrus centralis anterior.
subcallosus (pedunculus corporis callosi), part of the **Nucleus olfactorius medialis, 128,** 246
supramarginalis, **130**
temporalis inferior, **130**
medius, **130**
superior, **130, 184**
uncinatus. See **Uncus.**

Habenula (nucleus habenulæ, ganglion habenulæ), an important olfactory correlation center in the **Epithalamus, 177, 180,** 183, **184, 246**

Habit, physiological, 33, 330, 341
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Hearing, organs of. See Auditory apparatus.
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Hemianopsia, 314
Hemiplegia, motor paralysis of one side of the body, 319
Hemispheres, cerebellar, **129,** 209, **211**
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HERRICK, F. H., 64, 73
HERTZ, A. F., 100, 272, 278
HESS, C. L. VON, 265, 278
Hibernation, nerve cells in, 108
Hindbrain, a term which has been variously applied to the cerebellum, the cerebellum and pons, the medulla oblongata, and the entire rhombencephalon.
Hippocampal gyrus. See **Gyrus hippocampi.**
Hippocampus (hippocampus major, Ammon's horn, cornu Ammonis), a submerged gyrus forming the larger part of the **Archipallium,** or olfactory cerebral cortex, 243, 246, **248,** 308, 320, 344
commissure of. See **Commissure of hippocampus.**
minor. See **Calcar avis.**
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Histology, the study of **Tissues.**
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HODGE, C. F., 113
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HOLMES, G., 182, 188, 284, 293, 314, 336, 349
HOLMES, S. J., 293
Hormone, a specific chemical substance contained in an internal secretion and carried by the blood or lymph to another organ which it excites to functional activity, 111, 251
Horn (cornu), one of the three chief parts of the lateral ventricle—anterior, posterior, and inferior or middle; also applied to the gray **Columns** of the spinal cord.
of Ammon. See Hippocampus.
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Hunger, apparatus of, 95, 270
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HUSCHKE, teeth of, **223**
Hyodon tergissus, brain of, **340**
Hypophysis (pituitary body, pituitary gland), a glandular appendage to the ventral part of the hypothalamus; its posterior lobe is an outgrowth from the **Neural tube,** its anterior lobe is an ingrowth from the epithelium of the embryonic mouth cavity, **127, 128,** 179, 183
Hypothalamus, the ventral subdivision of the **Diencephalon,** containing the **Hypophysis** and the **mammillary Body,** an important olfactory correlation center, **126, 127,** 129, 131, 179, **180, 181,** 183, **190, 194,** 242, **246,** 247, 249, 276, 290

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Insula (island of REIL), a portion of the cerebral cortex which is submerged under the **Fossa lateralis, 181, 184,** 297, 308
Integration, the combination of different acts so that they coöperate toward a common end, 25, 37, 114, 122
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Intumescentia cervicalis (cervical enlargement), the enlargement of the spinal cord from which the nerves of the arm arise.
lumbalis (lumbar enlargement), the enlargement of the spinal cord from which the nerves of the leg arise.
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Island of REIL. See **Insula.**
Isthmus, a narrow segment of the brain forming the upper end of the **Rhombencephalon** (B. N. A.); it might better be regarded as merely the plane of separation between **Rhombencephalon** and **Cerebrum, 124, 126–128,** 129, 130, 155, 175
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affixa, a thin non-nervous part of the medial wall of the cerebral hemisphere attached to the thalamus and bordered by the lateral chorioid Plexus, **177**
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of GENNARI. See **Line of Gennari.**
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Lemniscus (fillet, laqueus), sensory fibers of the second order terminating in the thalamus.
acoustic. See **Lemniscus, lateral.**
bulbar, ascending sensory fibers of the second order from the medulla oblongata to the thalamus, including several different tracts, 171
gustatory. See **Lemniscus, visceral.**
lateral, the acoustic lemniscus, fibers from the cochlear nuclei to the colliculus inferior and thalamus, **123,** 171, **176, 178,** 180, 183, **190, 194,** 197, **204, 226**
Lemniscus, medial, ascending fibers of the proprioceptive system from the spinal cord to the thalamus, 150, **152, 169, 170,** 171, **176, 178,** 179, **180,** 183, **190,** 193, **194,** 196
optic, a term which might appropriately replace **optic Tract,** 235
spinal, ascending fibers of touch, temperature, and pain sensibility from the spinal cord to the thalamus. In the cord these fibers form two tracts, the dorsal and ventral spinothalamic tracts, 141, **144, 149,** 151, **152, 170, 176, 178,** 179, 183, **190,** 191, 193, 195, 196, **282, 283**
trigeminal, ascending sensory fibers of the second order from the sensory V nuclei to the thalamus, 151, **152,** 171, **176, 178,** 179, **180,** 181, 183, **190,** 191, 197
visceral, a name suggested for ascending secondary fibers from the nucleus of the fasciculus solitarius to higher cerebral centers, 172, 276
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Line of Baillarger, a stripe of tangential white fibers in the cerebral cortex; there is an outer and an inner line, **299, 304**
of Gennari, a stripe of tangential white fibers in the **Area striata** of the cerebral cortex; it is the outer **Line of Baillarger** in this area, 300, **302**
Lingula cerebelli, a small eminence on the ventral surface of the cerebellum where the anterior **medullary Velum** joins the **Vermis, 177, 212**

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Lizard, parietal eye of, 238
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of the lateral line (lobus lineæ lateralis), a highly differentiated part of the acoustico-lateral Area of fishes, 166
limbic. See **Gyrus fornicatus.**
occipital, 297, 316
olfactory (lobus olfactorius), the **olfactory Bulb**, its **Crus**, and the anterior part of the **Area olfactoria**; this is the B. N. A. usage; the term is sometimes applied to the **olfactory Bulb** alone and sometimes to the **Area olfactoria** alone.
optic. See **Colliculus superior.**
parietal, 297
pyriform (lobus piriformis), the lateral exposed portion of the olfactory cerebral cortex in lower mammals, bounded dorsally by the **Fovea limbica**; in man it is represented by the **Uncus** and part of the **Gyrus hippocampi**, 245
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Lungs, innervation of. See Respiratory apparatus.
Luys, body of. See body of Luys.
Lyra. See **Lyre of David.**
Lyre of David (lyra Davidis, psalterium), the posterior part of the **Fornix body**, including the **Commissura hippocampi.**

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Marsupial animals, cerebral cortex of, 243
Massa intermedia (commissura mollis, soft commissure, middle commissure), a band of gray matter connecting the medial surfaces of the two thalami across the third ventricle; it is not a true commissure, 128
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Matter, central gray. See **Gray, central.**
gray (substantia grisea), gray nervous tissue composed chiefly of nerve-cells and unmyelinated nerve-fibers, 116, 138
white (substantia alba), white nervous tissue composed chiefly of myelinated nerve-fibers, 116, 138

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Meatus, external auditory, **219**
Medial (medialis), nearer the median plane; opposed to lateral.
Median (medianus), lying in the axis or middle plane of the body or one of its members.
Medius, intermediate between two other parts.
Medulla oblongata (bulb), the **Myelencephalon** B. N. A.; the older and better usage includes the whole of the **Rhombencephalon** except the **Cerebellum** and **Pons, 115, 118–120, 123–129,** 130, 155, **166–170, 177, 178, 340**
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Metencephalon (hindbrain), the anterior part of the **Rhombencephalon,** including the **Cerebellum, Pons,** and intervening part of the **Medulla oblongata, 126–128,** 129
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cardiac, the muscle of the heart, a visceral muscle whose fibers are corss-striated, **99,** 162, 251, 263
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skeletal. See Muscles, somatic.
smooth or **unstriated,** visceral muscle whose fibers are not cross-striated, 92, **99**
somatic, striated muscles derived from the **Somites** of the embryo, skeletal muscles, **41,** 92, 98
spindle, a bundle of muscle-fibers, smaller than ordinary fibers, which are supplied with special nerve endings of the muscle sense in addition to typical motor **End-plates, 92**
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striated, composed of fibers having a cross-striped appearance; may be somatic or visceral, **41, 92,** 98, 99
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visceral, unstriated or striated muscles not derived from the **Somites** of the embryo; may be involuntary or voluntary, 92, 98, **99,** 162, 251
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Myel (myelon), the **Spinal cord.**
Myelencephalon (afterbrain), the posterior part of the **Rhombencephalon,** or that portion of the **Medulla oblongata** lying behind the **Pons** and **Cerebellum, 126, 127, 128,** 129, 130
Myelin, a fat-like substance formed as a sheath around the myelinated (medullated) nerve-fibers, 49
sheath, an envelope of **Myelin** around the **Axis-cylinder** of some nerve-fibers, **41,** 49, 116, 322
Myelogeny, the sequence of maturation of the **Myelin sheaths** of nerve-fibers in the development of the central nervous system, 322, 323, **324**
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Neothalamus (new thalamus), the phylogenetically new part of the **Thalamus,** which is a cortical dependency, 179–183, 294, 343
Nerve (nervus), any bundle of nerve-fibers outside the central nervous system, 29, 114
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Nervus. See Nerve.
Neural canal. See **Canal, neural.**
groove (medullary groove), the trough-like form assumed by the **Neural plate** during its invagination to form the **Neural tube.**
plate, a thickened plate of **Ectoderm** in early vertebrate embryos from which the **Neural tube** develops.
tube, the embryonic central nervous system when in the form of an epithelial tube, **114**, **124**, **126**, 136, 175, 199
Neuraxis, the central nervous system; also applied to the **Axon.**
Neuraxon. See **Axon.**
Neurenteric canal, in the embryo, a communication between the caudal end of the **Neural tube** and the digestive tract.
Neurilemma, the outer sheath of a peripheral nerve-fiber, **41**, 49
Neurite. See **Axon.**
Neurobiotaxis, 111
Neuroblast, an immature nerve cell, 40, **46**
Neurocyte. See **Neuron.**
Neurofibrils, delicate protoplasmic fibrils within the cytoplasm of the **Neuron**, 42, **48**, 49, 108
Neuroglia (glia), a supporting fabric of cells and horny fibers pervading the central nervous system, 39, 111, 214, 231, **232**, 300
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Neuromere, one of the segments of the embryonic **Neural tube.**
Neuron (neurocyte), a nerve cell; cf. Cell, 39–57, 102, **214**, **300–304**
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Nociceptor, a sense organ or **Receptor** which responds to injurious influences.
Node of Ranvier, an interruption of the **Myelin sheath** of a nerve-fiber, **41**
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Nucleus (2), a group of nerve-cells within the central nervous system; also called Nidulus and **Nidus**; cf. **Ganglion,** 116
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acoustic. See Nucleus, cochlear.
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amygdalæ (amygdala), a small mass of subcortical gray matter under the tip of the temporal lobe which forms part of the **Nucleus olfactorius lateralis, 181,** 240
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of auditory nerve. See Nucleus, cochlear, and Nucleus, vestibular.
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caudate (nucleus caudatus), one of the two large gray masses of the **Corpus striatum, 123, 177, 181, 184,** 185, 186, **248**
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of DEITERS, vestibular, 203, **204**
dentate, a large nucleus embedded within the cerebellar hemisphere from which the fibers of the **Brachium conjunctivum** arise, **123, 206,** 215, 226
dorsal, of Clarke (nucleus dorsalis of CLARKE or STILLING, CLARKE'S column), a longitudinal strand of neurons of the spinal cord whose axons enter the spino-cerebellar tracts, 141, 148, **149, 194**
of dorsal funiculus. See **Clava** and **Tuberculum cuneatum.**
dorsal, of vagus. See Nucleus of vagus, dorsal.
dorsalis thalami. See Nucleus anterior thalami.
dorso-lateral, of spinal cord, a collection of neurons in the ventral gray column which innervate the muscles of the limbs, **140**
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of fasciculus gracilis. See **Clava.**
of fasciculus solitarius, the visceral sensory nucleus of the VII, IX, and X cranial nerves, 164, **168,** 169, **170,** 263, **266,** 268, **269,** 272, **273,** 276
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globosus, 213
of glossopharyngeus nerve, 161, 164
habenulæ. See **Habenula.**

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interpeduncular, a nucleus lying between the cerebral peduncles which receives the habenulo-peduncular tract
of lateral lemniscus, **204**, **226**
lateralis thalami, 178–183, **185**, **190**, 193, **194**, 282, 319, 341
lattice, of thalamus. See Nucleus reticularis thalami.
lentiform (nucleus lentiformis, lenticular nucleus), one of the two large gray masses of the **Corpus striatum**, **123**, **181**, **184**, 185
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masticatory. See Nucleus of trigeminus, motor.
medialis thalami, **178**, 179, **181**, 183, **184**, **190**, **194**, 344
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motorius tegmenti, 199
of oculomotor nerve, **65**, **66**, 160, 162, 164, **168**, 175, **176**, **204**, **236**, 237, 276
olfactorius anterior, the anterior undifferentiated portion of the **Area olfactoria**, **246**
intermedius. See **Tuberculum olfactorium.**
lateralis, the lateral portion of the **Area olfactoria**, lying between the **olfactory Bulb** and the **Uncus**, **245**
medialis, the medial portion of the **Area olfactoria**, containing the **Septum** and **Gyrus subcallosus**, **245**
olivary. See Olive.
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Olive, accessory, **169**
inferior (oliva, nucleus olivaris, olivary body), a large gray center in the medulla oblongata which produces an eminence on its lateral surface, **123, 169, 170,** 172, **190, 194**
superior, a nucleus in the secondary auditory path embedded in the medulla oblongata dorsally of the pons, **63, 178, 204, 226**
peduncle of, **226**
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Operculum, the lobules of the frontal, parietal, and temporal cerebral cortex which cover the **Insula, 130, 184,** 297
Ophthalmencephalon, the retina, optic nerve, and visual apparatus of the brain.
Opossum, cerebral cortex of, 243
Optic apparatus. See Visual apparatus.
chiasma. See **Chiasma, optic.**
Optic tectum, an optic reflex center in the roof of the midbrain. See **Colliculus, superior.**
thalamus. See **Diencephalon.**
vesicle. See **Vesicle, optic.**
Oral, pertaining to the mouth, or directed toward the mouth, as opposed to **Caudal.**
sense of EDINGER, 247
Organ (organon), a part of the body with a particular function, 25
of CORTI. See **Organ, spiral.**
generative. See **Sexual organs.**
lateral line (neuromasts), sense organs in or under the skin of fishes and amphibians of intermediate type between tactile and auditory organs, 118–120, 159, 162, **163, 166,** 224, **225**
parietal. See **Parietal eye.**
pineal. See **Body, pineal.**
spiral (organon spirale), the organ of CORTI or receptor for sound in the **Cochlea,** 92, 221–224
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Palæëncephalon, the old brain, *i. e.*, all of the brain except the cerebral cortex and its **dependencies,** 123, 294
Palæothalamus (old thalamus), the phylogenetically old part of the **Thalamus,** present in animals which lack the cerebral cortex, 179, 181
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Pallium. See **Cortex, cerebral,** 242
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spastic, 319
Paraphysis, an evagination of the membranous roof of the telencephalon in front of the **Velum transversum** in some vertebrate brains.
Parietal eye (parietal organ, pineal eye, epiphyseal eye), a modification of the **pineal Body** in some lower vertebrates to form a dorsal median eye, **238,** 239
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optica hypothalami, the **optic Chiasma** and its environs, **127,** 129, 131
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Peduncle (pedunculus), a peduncle or stalk. See **Crus.**

Peduncle, cerebellar, one of the fibrous stalks by which the cerebellum is attached to the brain stem. There are three peduncles on each side: (1) the superior peduncle (**Brachium conjunctivum**), (2) the middle peduncle (**Brachium pontis**), (3) the inferior peduncle (**Corpus restiforme**), **123, 172, 177, 206,** 207
cerebral (pedunculus cerebri), the ventral part of the mesencephalon, **127–129,** 131, 175, **176, 177**
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Perikaryon, the protoplasm surrounding the nucleus in the **Cell body** of a **Neuron.**
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Perineureum, the connective-tissue sheath surrounding a peripheral nerve
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eye. See **Parietal eye.**
Pituitary body. See **Hypophysis.**
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Plate (lamina), a general term applied to any flat structure or layer; specifically to the six longitudinal bands or zones into which the **Neural tube** is divided as explained in the following definitions, **126**
dorsal (roof plate, Deckplatte), the unparied dorsal longitudinal epithelial zone of the **Neural tube;** it is non-nervous and in some parts of the adult brain is enlarged to form a lamina epithelialis, 133, **167**
dorso-lateral (alar plate, wing plate, epencephalic region, Flügelplatte), one of a pair of dorso-lateral longitudinal zones of the **Neural tube;** it gives rise to the dorsal gray column of the spinal cord and to the sensory centers of the brain, 125, **126, 167**
floor. See **Plate, ventral.**
neural. See **Neural plate.**
roof. See **Plate, dorsal.**
ventral (floor plate, Bodenplatte), the unpaired ventral longitudinal zone of the **Neural tube;** it is originally non-nervous, but in the adult is invaded by the **ventral Commissure, 167**
ventro-lateral (basal plate, hypencephalic region, Bodenplatte), one of a pair of ventro-lateral longitudinal zones of the **Neural tube;** it gives rise to the ventral gray column of the cord and to the motor centers of the brain, 125, **126, 167**
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Pleasantness, Pleasure. See Affection.
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Plexus, choroid (plexus chorioideus), highly vascular **Pia mater** attached to non-nervous epithelial plates which are crumpled and thrust into the brain **Ventricles,** 133

Plexus, choroid, lateral, the choroid plexuses of the lateral ventricles of the cerebral hemispheres, 133, **248**
of fourth ventricle (plexus chorioideus ventriculi quarti), the choroid plexus which forms the roof of the fourth ventricle, 133, 177
of third ventricle (plexus chorioideus ventriculi tertii), the choroid plexus which forms the roof of the third ventricle, 133, **181**
ganglionic, of sympathetic nervous system, an entanglement of sympathetic nerves and ganglion cells; most of the nervous plexuses enumerated in the following list are ganglionic plexuses of this type, 252, **253,** 270
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Posterior, as used in this work means toward the tail end of the body; as used in the B. N. A. tables it means toward the **dorsal** side, 125
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Process, axis-cylinder. See **Axon.**
ciliary, of eyeball, 155, 160, 259, 276
protoplasmic. See **Dendrite.**
Processus reticularis, the **Formatio reticularis** of the spinal cord, 137, **139**
Projection centers, those parts of the cerebral cortex which receive or give rise to **Projection fibers;** cf. **Center, cortical,** 181, 308, **317, 318,** 319–325, 343
fibers, fibers which connect the cerebral cortex with the brain stem, **178,** 180, **181, 184,** 186, 298, 318–325
Proprioceptor, a sense organ lying within the deep tissues of the body for the coördination of somatic reactions, 82, 92
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Prosencephalon (forebrain), the **Diencephalon** and **Telencephalon;** sometimes applied to the **Cerebral hemispheres** only, 126–129, 175

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Protopathic sensibility, a primitive type of diffuse cutaneous sensibility, especially on hair-clad parts, 89, 90, 197
Protoplasm, living substance, 25, 74, 102
nervous, 39, 74, 102
Protozoa, one-celled animals, 25, 352
Psalterium. See **Lyre of David.**
Pseudocœle. See **Cavum septi pellucidi.**
Psychogenesis, the development of mind, 287, 330, 338–354
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Pulvinar, a visual center in the thalamus, 164, **177, 178,** 180, 183, **184,** 234, 238, 320, 344
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Purple, visual, 233
Putamen, a part of the **Nucleus lentiformis,** 185
Pyramid (pyramis), an eminence on the ventral surface of the medulla oblongata produced by the pyramidal tract and from which the latter receives its name, **123, 169**
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Quale, a quality pertaining to anything; specifically a quality of sensation or other conscious process, 279, 291, 345, 347, 349

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olfactory, the olfacto-cortical tracts; the term has also been applied to various subcortical olfactory tracts, 323
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Ramus communicans, a communicating branch between the ganglia of the **sympathetic Trunk** and the roots of the spinal nerves, **135, 136,** 252, **253, 256,** 260
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time, the time required for response to stimulation, 104, 288
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Receptor, a sense organ, 26, 40, 74
contact, a sense organ adapted to respond to impressions from objects in contact with the body; opposed to **distance Receptor.**
distance, a sense organ adapted to respond to impressions from objects remote from the body, 23
Recess, epitympanic, **219**
infundibular, **127, 128**
lateral, the widest part of the **fourth Ventricle** under the cerebellum.
optic, the depression in the lateral wall of the diencephalon formed by the evagination of the **optic Vesicle, 126–128**
utricular. See Utricle.
Reflex act, a simple form of **invariable Behavior** requiring a nervous system, 26, 32, 59, 117
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ROLANDO, fissure of. See Sulcus centralis.
gelatinous substance of. See **Substantia gelatinosa Rolandi.**
Root (radix), a nerve root, or the part of a nerve adjacent to the center with which it is connected; in the case of spinal and cranial nerves, the part lying between the cells of origin or termination and the ganglion.
anterior. See **Root, ventral.**
dorsal (radix dorsalis, posterior root, radix posterior), the dorsal or sensory **Root** of a spinal or cranial nerve, **136**, **138–140**, **143**, **144**, **146**, **149**, **164**, **165**, 253, **254**, 255, **256**
posterior. See **Root, dorsal.**
spinal, composition of, **136**, 145, **146**, 161, **164**, **165**
ventral (radix ventralis, radix anterior), the ventral or motor root of a spinal or cranial nerve, **136**, **138–140**, **143**, **144**, **164**, **165**, 199, 255
Rostral, pertaining to the beak or snout, or directed toward the front end of the body as opposed to **Caudal.**
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organ. See **Receptor.**
Sentiments. See Affection.
Septum, the medial wall of the cerebral hemisphere between the **Lamina terminalis** and the **olfactory Bulb;** in man its upper part is thin and forms the **Septum pellucidum,** 246, 344
dorsal median, of cord. See Fissure, dorsal.
pellucidum, a thin sheet of nervous tissue forming a portion of the medial wall of each cerebral hemisphere between the **Corpus callosum** and the **Fornix, 177**
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STILLING, dorsal nucleus of. See Nucleus, dorsal, of CLARKE.
Stimulus, a force which excites an organ to activity, 59, 74
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Stria acustica. See **Stria medullaris acustica.**
of BAILLARGER. See **Line of Baillarger.**
of GENNARI. See **Line of Gennari.**
longitudinalis (stria of LANCISI, nerve of LANCISI), slender bundles of nerve-fibers running along the dorsal surface of the **Corpus callosum** in the floor of the longitudinal fissure.
medullaris acustica, secondary acoustic fibers arising in the dorsal cochlear nucleus and decussating across the floor of the fourth ventricle to reach the opposite **lateral Lemniscus, 226**
thalami, a band of fibers accompanying the **Tænia thalami** along the dorsal border of the thalamus, containing the tractus olfacto-habenularis, tractus cortico-habenularis, and other fibers, **177, 180, 181,** 183, **246**

Stria olfactoria intermedia, a secondary olfactory Tract from the olfactory Bulb to the Tuberculum olfactorium, most of its fibers first crossing in the anterior Commissure, 245
lateralis, a secondary olfactory Tract from the olfactory Bulb to the Nucleus olfactorius lateralis, 245
medialis, a secondary olfactory Tract from the olfactory Bulb to the Nucleus olfactorius medialis, 245
semicircularis. See **Stria terminalis.**
terminalis (stria semicircularis, old term, tænia semicircularis), a correlation tract between the Nucleus amygdalæ of the lateral olfactory Area and the medial olfactory Area, **177, 298**
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Subconscious mind. See Unconscious cerebration.
Subiculum, that part of the Gyrus hippocampi which broders the fissura hippocampi; sometimes applied to the whole of this gyrus, **248**
Substance, black. See **Substantia nigra.**
chromophilic (NISSL substance, tigroid substance, or bodies, or granules), a proteid substance typically present in the cytoplasm of nerve-cells, **41, 42, 43, 47, 48, 50, 51, 105, 108, 147, 318**
Substance, gray. See **Matter, gray.**
perforated. See **Substantia perforata.**
white. See **Matter, white.**
Substantia alba. See **Matter, white.**
gelatinosa Rolandi (gelatinous substance of ROLANDO), an area of Neuropil bordering the dorsal gray column of the spinal cord; sometimes also applied to the nucleus of the spinal V tract in the medulla oblongata, **139**
grisea. See **Matter, gray.**
nigra (black substance), an area of gray matter immediately dorsal of the **Basis pedunculi**, functionally related to the cortico-pontile tracts, **176, 180, 183, 236**
perforata, anterior (anterior perforated substance or space), a region on the ventral surface of the brain in front of the optic Chiasma which is pierced by many small arteries, **123, 129, 245,** 344
posterior (posterior perforated substance or space), a region on the ventral surface of the brain between the Bases pedunculi which is pierced by small arteries, **129**
Subthalamus, the ventral part of the Thalamus, 179, **180, 181,** 183, **190, 194,** 344
Sulcus, in the cerebral cortex, a superficial fold not involving the entire thickness of the brain wall; cf. **Fissure,** 130, **297**
anterior parolfactory, **128**
central (fissure of ROLANDO, cruciate sulcus), **128, 130,** 314, **315**
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cruciate. See Sulcus, central.
frontalis, inferior, **130**
superior, **130**
horizontalis, **211**
magnus, **212**
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Sulcus, limiting (sulcus limitans), a longitudinal groove on the ventricular surface of the embryonic brain separating the dorsolateral sensory **Plate** from the ventro-lateral motor **Plate**, 37, 125, **126**, **167**, 199
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Summation, central. See **Conduction, avalanche,** and **Reinforcement.**
of stimuli, the enhancement of effect by repeated stimulation, 62, 65, 66, 216, 234, 244, 288, 291, 303, 344
Suprasegmental apparatus, the cerebral cortex and cerebellum with their immediate dependencies, 122, 131, 155, 172, 205
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fissure of. See **Fissure, lateral.**
fossa of. See **Fossa lateralis.**
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Sympathetic nervous system. See Nervous system, sympathetic.
Synapse, the place where the nervous impulse is transmitted from one neuron to another, **52**, **53**, 54–57, 103, 108, 117, **244**, **303**, 331
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time of transmission through, 57, 105
Synergic muscles. See **Muscles, synergic.**
System, functional, all neurons of common physiological type. Most peripheral nerves contain several components belonging to different systems, 157–170
Tabanus bovinus, nervous system of, **31**
Tænia, the line of attachment of a membranous part to a massive part of the brain wall; formerly applied also to some fiber tracts, as Tænia semicircularis = **Stria terminalis**, and Tænia thalami = **Stria medullaris thalami**
chorioidea, the line of attachment of the lateral **choroid Plexus** to the medial wall of the cerebral hemisphere. (This portion of the medial wall is adherent to the thalamus, forming the **Lamina affixa**), **177**
fornicis, the line of attachment of the lateral **choroid Plexus** to the **Fimbria** of the **Fornix.**
thalami, the line of attachment of the **Tela chorioidea** of the third ventricle to the dorsal margin of the thalamus. This name was formerly applied to a band of fibers, the **Stria medullaris thalami**, which borders the tænia.
ventriculi quarti, the line of attachment of the membranous roof of the fourth ventricle to the medulla oblongata, **169**
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Taste, apparatus of. See Gustatory apparatus.
bud, **96**, 156, 244, 272–276
peripheral nerves of. See Nerves, gustatory.
Taxis. See **Tropism.**
Tectum mesencephali, the roof of the midbrain, comprising the **Colliculus superior** (tectum opticum) and the **Colliculus inferior**, **176**
optic. See **Colliculus, superior.**
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of HUSCHKE, **223**
Tegmen ventriculi quarti, the roof of the fourth ventricle, formed chiefly by the **Velum medullare anterius**, the **Velum medullare posterius**, and the **Plexus chorioideus ventriculi quarti.**

Tegmentum, the dorsal part of the **cerebral Peduncle** between the **Basis peddnculi** and the **Aqueduct of Sylvius**; often described as also extending backward into the corresponding part of the medulla oblongata, 172, 199
Tela, any thin non-nervous part of the brain wall.
chorioidea, that portion of the **Pia mater** which covers any thin non-nervous part of the brain wall, including the **choroid Plexuses**, 133
Telencephalon (endbrain), the anterior end of the embryonic **Neural tube** and its adult derivatives, comprising chiefly the cerebral hemispheres and **Lamina terminalis, 126–128**, 130, 131, 175
medium, that portion of the embryonic **Telencephalon** which is not evaginated to form the cerebral hemispheres; it comprises chiefly the **Lamina terminalis** and **Pars optica hypothalami.**
Telodendron, the terminal branched end of a **Dendrite**; sometimes applied also to that of an **Axon**; cf. **Terminal arborization.**
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Tendon, nerve endings in, 93
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Tentorium cerebelli, a transverse fold of **Dura mater** between the cerebellum and the cerebral hemispheres, 132
Terminal arborization, the branched end of an axon; sometimes applied also to that of a **Dendrite, 41**
Terminology. See Nervous system, terminology of.
Testes. See **Colliculus, inferior.**
Thalamencephalon. See **Diencephalon.**
Thalamus, the middle and larger subdivision of the **Diencephalon**, sometimes applied to the entire diencephalon and called Thalamus opticus, **66, 120, 123, 126**, 129–131, **152**, 177–183, **190, 194**, 230, **236**, 283–285, 313, 438
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Thorns of dendrites, 305
Threshold, the minimal stimulus which will excite an organ to activity, 75, 77, 86, 97, 142, 189, 244, 283–285
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Tigroid bodies, substance, or granules. See **Substance, chromophilic.**
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Time, central. See Pause, central.
latent. See Pause, central.
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Tissue, the cellular fabric of which the body is composed, 25
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Tract (tractus), a collection of nerve-fibers of like origin, termination, and function; cf. **Fasciculus**, 28, 106, 139, 341
association; cf. Fibers, association, **61**, 67, **298**, 321
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comma. See Fasciculus interfascicularis.

Tract, cortico-bulbar, **176, 184,** 186, **198,** 319
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cortico-oculomotor, **184**
cortico-pontile, **176, 184,** 186, **206,** 207, 208, 323
cortico-rubral, **170, 185,** 323
cortico-spinal (fasciculus cerebrospinalis, B. N. A., pyramidal tract), the voluntary motor path from the precentral gyrus of the cerebral cortex to the spinal cord, where it divides into lateral and ventral parts, 71, 138, **140,** 141, 151, **152, 169, 170, 176,** 183, **184,** 186, **198, 206,** 216, 317–320, 323, **347,** 348
lateral (fasciculus cerebrospinalis lateralis, B. N. A., lateral or crossed pyramidal tract), **140, 141, 152**
ventral (fasciculus cerebrospinalis anterior, B. N. A., ventral or direct pyramidal tract, column of TÜRCK), **140,** 141, **152**
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habenulo-peduncular (fasciculus retroflexus, MEYNERT'S bundle), **180, 246**
of HELWIG. See Tract, olivo-spinal.
internuncial, a fiber tract connecting two nuclei or centers, 69
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of MEYNERT. See Tract, habenulo-peduncular.
Tract of MONAKOW. See Tract, rubro-spinal.
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olfactory (tractus olfactorius), olfactory fibers of the second order passing from the **olfactory Bulb** to the nuclei of the **Area olfactoria.** See **Stria olfactoria, 129, 180, 243, 244, 245, 246**
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olivo-cerebellar, **169, 194, 206,** 208
olivo-spinal (HELWIG'S bundle, tractus triangularis), **140,** 141
optic (tractus opticus), that portion of the optic path which passes between the **optic Chiasma** and the optic centers in the thalamus and midbrain. (The term might properly be extended to include also the so-called **optic Nerve**), **123, 129, 176, 181,** 183, 234, 235, **236**
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dorsal (fasciculus cerebello-spinalis, B. N. A., direct cerebellar tract, FLECHSIG'S tract), **140,** 141, **149, 170, 194, 206,** 208

Tract, spino-cerebellar, ventral (part of GOWER'S fasciculus, or Fasciculus antero-lateralis superficialis, B. N. A.), **140**, 141, **149**, **170**, **194**, **206**
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Transmission of nervous impulse. See Conduction, nervous.
Trapezoid body. See **Body, trapezoid.**
Trigonum habenulæ, a triangular area at the posterior end of the **Habenula**, **177**
hypoglossi (eminentia hypoglossi), a ridge in the floor of the fourth ventricle produced by the XII nucleus, **168**, **170**
olfactorium, a triangular expansion of the **Crus olfactorium** from which the **Striæ olfactoriæ** arise
vagi. See **Ala cinerea.**
Tropism, a simple form of invariable behavior not requiring a nervous system, 60
TROTTER, W., 90, 101, 189
Trunk (truncus), the main stem of a nerve from which the branches (rami) are given off. See **Nerve.**
Trunk, sympathetic (ganglionated sympathetic cord, sympathetic chain, vertebral sympathetic chain), a strand of sympathetic nerves and ganglia extending along each side of the vertebral column, **115**, 252, **253**
Tube, auditory (Eustachean tube), 219
neural. See **Neural tube.**
Tuber cinereum, a gray eminence forming the ventral part of the **Hypothalamus**, **128**, **129**, 179, 183, 344
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Tubercle, anterior, of thalamus, an eminence on the dorsal surface formed by the Nucleus anterior thalami, **177**
Tuberculum acusticum of fishes (part of the **Area acustico-lateralis**), 162, **163**, 166, **225**
of mammals (the dorsal cochlear nucleus), **226**
cinereum, an eminence on the lateral aspect of the medulla oblongata produced chiefly by the spinal V tract and its nucleus.
cuneatum, an eminence on the dorsal surface of the lower end of the medulla oblongata laterally of the **Clava** produced by the nucleus of the **Fasciculus cuneatus**, 140, **152**, **194**, **205**, **206**
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olfactorium (lobus parolfactorius of EDINGER), the intermediate **olfactory Nucleus**, lying in the **Substantia perforata anterior**; cf. **Area olfactoria**, **245**, **246**, 308
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Utricle (utriculus, recessus utriculi), part of the membranous labyrinth of the inner ear, **92**, **202**, **219**, **220**, **224**, **225**
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Valve of VIEUSSENS. See **Velum medullare anterius.**
Valvula cerebelli. See **Velum medullare anterius.**
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Veins, nerves of. See **Vasomotor apparatus.**
Velocity of nervous conduction. See Nervous impulse, velocity of.
Velum anticum. See **Velum medullare anterius.**
interpositum, the **Tela chorioidea** of the third ventricle.
medullare anterius (or superius), a thin portion of the brain wall containing a few myelinated fibers which forms the roof of the fourth ventricle in front of the cerebellum, **128**, **168**, **212**
posterius, a thin portion of the brain wall containing a few myelinated fibers which forms a small part of the roof of the fourth ventricle immediately behind the cerebellum.
superius. See **Velum medullare anterius.**
Velum transversum, a transverse fold of the **Tela chorioidea** which marks the boundary between the **Diencephalon** and the **Telencephalon** in the embryonic brain.
Ventral, on the front or belly side of the body, termed **Anterior** in the B. N. A. lists, 125
Ventricle, a cavity within the brain and spinal cord derived from the lumen of the embryonic **Neural tube.**
fifth. See **Cavum septi pellucidi.**
first. See **Ventricle, lateral.**
fourth (ventriculus quartus, metacœle), the ventricle of the medulla oblongata, **128**, 129, **166**, **168**, **293**
lateral (paracœle), the ventricle of each cerebral hemisphere; these are also called first and second ventricles, 129, **181**, **184**, **295**
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third (ventriculus tertius, diacœle), the ventricle of the diencephalon, 129, **177**, **184**, **295**, 296
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optic, an outgrowth from the lateral wall of the diencephalon which forms the nervous part of the eyeball. It first assumes the form of a simple hollow sphere, the primary optic vesicle, which later collapses to form a two-layered optic cup, or secondary optic vesicle, **124**, **126**, **230**
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